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Stereotypical behaviours in the striped mouse *Rhabdomys pumilio*: evaluating the coping hypothesis

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa, in fulfilment of the requirements for the degree of Master of Science

Johannesburg 2005

Declaration

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg, South Africa. It has not been previously submitted of any degree or examination in any other university.

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Mathew van Lierop
March 2005

Abstract

Stereotypic behaviours are repetitive invariant behaviours that serve no obvious purpose and are common in both domestic and non-domestic captive animals. Stereotypies are regarded as indicators of poor welfare although the growing body of work pertaining to these behaviours has challenged many previously held notions of stereotypy. The most widely accepted, although frequently contested, hypothesis used to explain stereotypies is the coping hypothesis, which states that animals perform stereotypies to cope with the stress of adverse environments.

The aim of my study was to investigate the fitness effects of stereotypy, and whether or not environmental enrichment protocols were effective in reducing or eliminating stereotypy in the adult striped mouse *Rhabdomys pumilio*. Both of these experiments were designed to evaluate the coping hypothesis. I intentionally used wild caught and F1 individuals to eliminate any potential captive selection bias that may exist in extant captive populations that could affect interpretation of fitness. For the first aim, 40 breeding pairs were assigned to one of four treatments: 1) stereotypic female and stereotypic male (S-S); 2) stereotypic female and non-stereotypic male (S-NS); 3) non-stereotypic female and stereotypic male (NS-S); and 4) non-stereotypic female and non-stereotypic male (NS-NS). Compared to non-stereotypic females, stereotypic striped mice females had better reproductive output, including larger litter size, higher growth rate, higher litter survival, shorter interlitter interval and shorter time to first litter. Reproductive success was higher in S-S and S-NS pairs, indicating that genetic and maternal effects jointly determined fitness in striped mice. Unlike other published research, maternal mass was not a predictor of fitness. For the second aim, I housed 20 non-stereotypic and 20 stereotypic striped mice (equal sex ratio) in barren cages for 60 days, and transferred them to enriched cages, and repeated this experiment with striped mice housed initially in enriched cages and transferred to barren cages. While there was a measurable reduction in stereotypy in individuals transferred from barren to enriched environment cages, no increase in stereotypy was noted in striped mice transferred from enriched to barren cages. These findings appear to concur with the coping hypothesis, that stereotypies become perseverative (e.g. bad habits) and difficult to disrupt. Non-stereotypic striped mice were not influenced by the swap.

I conclude that the expression of stereotypy is a potential sign of positive welfare and that it may be worthwhile to specifically elicit stereotypic behaviours in order to improve the welfare, and in certain cases, breeding success, of captive animals. Moreover, I maintain that where

necessary, effort should be applied to combating stereotypies before they arise, rather than attempting to eliminate them once they have actually developed.

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Chapter 1 General Introduction

1.1 Definition

Stereotypic behaviours are defined as repetitive, invariant acts that appear to lack any goal or function (e.g. Ödberg 1978; Mason 1991a), and may be considered the outcome of problematic organism-environment interaction (Carlstead 1998). Whereas stereotypies may be easily and intuitively identified upon observation, the diversity of their form and duration of expression is vast, their defining behavioural characteristics are vague, their distinction from other (normal) behaviours is blurred, and their apparent lack of purpose is largely based on subjective biases of human observers (e.g. Mason & Latham 2004). This may be because of our relatively poor understanding of the physiology and psychology of these behaviours. Stereotypies are thus usually first identified because of their qualitatively abnormal or undesirable appearance (Lawrence & Rushen 1993), and are perhaps the most commonly recognised abnormal behaviour in captive animals (Garner, in press). Although stereotypic behaviours are difficult to define, the frequency with which they arise in captive animals, in both diversity of species and numbers of individual animals, have made them the focus of many studies (see Mason 1991a).

The objective (the repetition of invariant behaviours) and subjective (apparent lack of goal or function; Dantzer 1991) definitions of stereotypy have generated much controversy. Many behaviours which are not stereotypic are at times repetitive or invariant (e.g. ritualised aggression, sexual behaviour, foraging and feeding; Mason 1991a). In fact, the characteristics of play, which include “apparently purposeless activity with no immediate adaptive goal”, “utilising species-typical motor programmes”, “exaggerated in intensity or number of repetitions” (Gamble & Cristol 2002, p339), are virtually identical to those for stereotypy. Moreover, as stereotypic behaviours often arise from species-typical behaviours, most behaviours that may be interpreted

as being stereotypies can be categorised along a continuum from completely normal to irrefutably stereotypic, and may even be incorporated into otherwise normal behaviour patterns (Mason & Mendl 1993).

1.2 Causal mechanisms of stereotypy

Determining the specific causal mechanism of stereotypic behaviour in captive species is not simple, since it is not clear what brings about the onset of stereotypy. A confounding aspect of investigating causal mechanisms is that stereotypic behaviours do not develop in all individuals of a species housed in a specific environment (Mason 1991b) and are affected by both age and context of the animal (Mason 1993a). This lack of causal commonality is probably fundamental to the differing opinions and proposed hypotheses that will be further explored in this dissertation. Various mechanisms have been attributed to causing stereotypy, such as housing in barren environments (Sørensen 1987), routine or restricted feeding (Falk 1971; Lawrence & Terlouw 1993), social deprivation (Sahakian *et al.* 1975) and other situations that elicit frustrations (Ödberg 1978; Rushen 1985; Wiedenmayer 1997). The success of various enrichments (techniques applied in captive animal management to enhance the captive environment and provide captive animals with choice) in reducing the expression of stereotypy indicates that these behavioural needs can be met, hence suggesting a number of clear causal mechanisms that underlie stereotypy (Young 2003). The expression of true stereotypy is observed exclusively in captive animals and the underlying mechanisms are likely to be psychological responses to past or present stress (Mason 1991a; Rushen *et al.* 1993; Cooper & Nicol 1996).

These proposed psychological mechanisms are, however, not the only identified causes of stereotypy. Wiepkema (1987) reported that, in domestic veal calves fed only on milk, stereotypies may not necessarily always be expressed in response to stress. This research

suggested that non-nutritive sucking, which was identified as a stereotypy, affected digestive hormone secretion and that a physiological/biochemical response other than those involved in direct stress response was responsible for the expression of this behaviour. Those calves that did perform the stereotypy had fewer stomach ulcers than those that did not. Similarly, Baxter & Plowman (2001) proposed that in giraffe, stereotypies were abated through the addition of fibre that resulted in an increase in ruminating and a decrease in stereotypy. These specific physiological causes of stereotypy give some indication that not all stereotypies are related to environmental stresses. Stereotypies can be artificially induced by psychostimulant drugs (e.g. laboratory rats; Mittleman *et al*. 1991; Abrams & Bruno 1992), which does allude to a biochemical link. The vast diversity of expression underlies the potential for varied, species-appropriate underlying causes, potentially based on underlying relevant physiological needs.

1.3 Development of stereotypy

Unlike the causal mechanisms of stereotypy, the development of stereotypies has perhaps received less emphasis in the literature. In humans, stereotypies are related to pathological disorders and may develop in patients suffering from mental retardation, autism, schizophrenia (Frith & Done 1990) and drug stimulants (Robbins *et al.* 1990). The occurrence of stereotypies related to abnormal development was first conclusively reported by Berkson (1967) in isolation-reared laboratory primates where self-directed stereotypies were often observed (although alluded to by Foley 1934). Holzapfel (1938) was one of the first researchers to describe what we now call ‘stereotypies’ in zoo animals. Over time, the term ‘cage stereotypies’ (Ridley & Baker 1981) was coined. These stereotypies are thought to be environmentally induced, where animals are physiologically normal but the environments in which the animals live are less than optimal

(Carlstead 1998; Mason 1991a, b). With the increasing interest in stereotypies, further and varied research was undertaken, and Wurbel and Stauffacher (1998) found that laboratory mice weaned prematurely or mice that were under-weight at weaning, performed higher rates of stereotypy when they were adults, possibly reflecting the effects of some physical retardation.

There is a growing body of evidence that stereotypy is genetically transmitted, as revealed by studies in bank voles *Clethrionomys glareolus* (Schoeneker & Heller 2000), striped mice *Rhabdomys pumlio* (Schwaibold & Pillay 2001) and mink *Mustela vison* (Jeppesen *et al*. 2004). However, the importance of non-genetic factors (e.g. maternal behaviour) cannot be ruled out. Stereotyping mothers may show deviating nursing behaviour, which could influence the development of stereotypies in their offspring, especially if stereotypic behaviour is partially influenced by frustrating or stressful experiences in early life (Wurbel & Stauffacher 1997; Schoenecker *et al*. 2000; Jeppesen *et al.* 2004). Future studies should perhaps consider the interplay of genetic and environmental factors on the expression of stereotypies.

1.4 Function of stereotypies

The function of stereotypies is not clearly understood. It is evident that the term ‘stereotypy’ covers an extensive range of different behaviours that develop from a spectrum of normal behaviours, ranging from pacing in large cats (Carlstead 1998) to bar chewing in rodents (Garner & Mason 2002) to tongue play in giraffe (Tarou *et al*. 2003). The coping hypothesis proposed by Rushen (1993) is one explanation for the function of stereotypies. This hypothesis states that an organism develops stereotypy to cope with the adverse environment in which it is housed (Rushen 1993). Opponents to the coping hypothesis argue that not all forms of stereotypy are responses to stress (Mason 1991a; Cooper & Nicol 1993). However, experimental studies

have failed to reproduce the stress reducing effects of stereotypy (see Schouten *et al*. 1991; Terlouw *et al*. 1991) and evidence of the coping hypothesis remains inconclusive. The application of the coping hypothesis in its broadest definition may still hold true for all incidences of expression of stereotypy. In this light, the 'coping' may not necessarily always be related to stress, or stress inducing environments, but rather related to any particular inadequacy in an animals' environment resulting in a form of coping response.

Because of the absence of stereotypies in nature, their function is not always known and they may be ultimately functionless. However, stereotypies may have an ultimate function if: (1) the observer has not yet identified the benefits of the behaviour (Mason 1991a); or (2) the potential benefit is accrued long after the behaviour has been performed. Alternatively, behaviours may be ultimately functionless, but still serve a proximate purpose if: (1) they are relatively independent of their original goal, or are performed in an inappropriate environment; or (2) the behaviour is self-reinforcing (has an internal consequence which cannot be directly observed; Mason 1991a). The performance of stereotypies may have immediate benefits (e.g. an adequate substitute for an otherwise thwarted behaviour; Vestergaard *et al*. 1990), be associated with the release of endogenous opioids (Spruijt *et al.* 2001), and/or be a coping response (Rushen 1993), but may be non functional or even ultimately dysfunctional.

1.5 Stereotypic behaviours and fitness

Mason *et al.* (1995) reported that young of high-stereotyping female farmed mink show lower weight gain than young from low-stereotyping females. They attribute these differences to inherent differences between the young in each group (i.e. by channelling energy into activity rather than growth) and to highly-stereotypic females using energy to perform stereotypies rather

on parental care. Breeding experiments of this nature provide an opportunity to begin to compare the fitness of individuals with and without stereotypy. However, for these breeding experiments to provide valid results, certain fundamentals need to be determined. G. Mason (pers comm.) hypothesised that in breeding experiments using stereotypic and non-stereotypic species, those that stereotypy will be inherently more fit themselves, due to their higher levels of physical activity and reduced obesity, and thus any potential difference in reproductive success can be attributed to this (this is contrary to opinions expressed in the work mentioned above in mink). An alternative argument that can be considered through these types of breeding experiments is if stereotypic animals have an inherent need to stereotypy, they may not nurture their young optimally, so while they could (should Mason's hypothesis be valid) produce more young, they would not necessarily rear these young as effectively as non-stereotypic parents (see Mason *et al.* 1995). In order to attempt to remove these potential biases in breeding experiments, an attempt to assess the fitness of the mother should be undertaken.

To further confound research undertaken on the relationship between breeding success and stereotypic behaviours, Jeppesen *et al*. (2004) reported, in a fitness context, the converse to Mason *et al*. (1995). Jeppesen *et al*. (2004) found that high- stereotypic mink had higher reproductive success, and produced more offspring than low-stereotypic mink. Thus it could be concluded that this high-stereotypic group had a higher fitness than the-low stereotyping mink. However, Jeppesen *et al*. (2004) also reported that fitter mink – those that stereotypy more - weighed less, and that the decreased reproductive capacity of non-stereotypic mink may relate to them being obese.

Ultimately, regardless of the underlying reasons why stereotypic individuals have a different fitness, if in fact this is the case, the conclusion is that stereotypic behaviour does

influence fitness. Hence purely from a practical zoo and farm animal husbandry based perspective, most notably with reference to production, debates of this nature may largely be intellectual and of little practical benefit.

1.6 Stereotypies and welfare

Extensive assessment of stereotypic behaviours has been undertaken in terms of viewing these behaviours as an indicator of poor or substandard welfare, frequently with emphasis on the coping hypothesis (Meyer-Holzapfel 1968, Broom 1983; Mason 1991a; Mason & Latham 2004). Further confirmation of this view is that the frequency of expression of stereotypic behaviours is much greater in captive animals housed in substandard environments (Mason 1991b; Shepherdson *et al* 1998). However, the lack of an apparent function for stereotypies may reflect our current state of knowledge, rather than the intrinsic property of the behaviour (Duncan *et al*. 1993), and we cannot assume *de facto* that stereotypic behaviour reflects poor welfare. With reference to this, Mason and Latham (2004) advise that stereotypies should always be taken as a warning of potential suffering, but are not necessarily a conclusive indicator of such.

Whilst the coping hypothesis is still a popular explanation for stereotypies, results from studies investigating how stereotypies may reduce physiological responses to stress, based on demonstrable, measurable output (e.g. raised corticosteroids) have been mixed (Mason 1991b). Mason and Latham (2004) reviewed stereotypic behaviours and their association with welfare and report that stereotypy is linked with good or neutral welfare with almost the same frequency as it is associated with poor welfare. However, Clubb and Mason (2003) claim that there are direct correlations between the size of the territory of large carnivores and the expression of stereotypy within the confines of a zoo environment, and attribute this, rather inexplicably,

directly to poor welfare. In an earlier study, Wurbel *et al*. (1998) express strong doubts about the validity of the coping hypothesis, but do not rule it out completely. Their conclusions nevertheless are based solely on wire gnawing behaviour in laboratory mice and may not necessarily be reflected in all forms of stereotypic behaviours, nor in all scenarios where the coping hypothesis might well be valid. There may be, for example, differing eliciting situations for different stereotypies, or physiological inadequacies as detailed above. In addition, although stereotypic-eliciting situations are likely to compromise welfare, Mason (1991b) argues that stereotyping individuals usually have improved welfare compared with non- or low-stereotyping animals in the same circumstances. Again, this is not always the case as is evident in the review by Latham and Mason (2004), indicating that whilst some stereotypies may enable an animal to cope and hence improve its individual welfare, it is exceedingly unlikely that coping is their sole function and that as in the examples above other functions may exist.

A further complication when addressing stereotypies is that the performance of the stereotypy may not be related to its original causes (Cooper & Nicol 1996), and may become established within the animal's behavioural repertoire (Duncan and Wood-Gush 1972) and persevere in environments different to the one eliciting the stereotypies (e.g. Fentress 1973; Dantzer 1986). For example, the transferring of bank voles *Clethrionomys glareolus* from barren to enriched cages reduces the incidence of stereotypies, but is less effective in older animals (Cooper & Nicol 1996). Thus, the current expression of stereotypy is indicative of previous problematic organism-environment interactions and in these cases the stereotypies are most probably unreliable indicators of the animal's current state of welfare (Mason & Latham 2004).

1.7 My research

For my study, I investigated the reproductive capacity of striped mice *Rhabdomys pumilio* in which both parents were either stereotypic or non-stereotypic, and in which one of the parents was stereotypic. Research into the effects of stereotypic behaviours on a measurable output of fitness is surprisingly limited and has not been undertaken on wild caught or F1 generation animals (but see Cooper & Nicol 1996), which my research addresses. I also studied the effects of enrichment on the expression of stereotypic behaviour in striped mice raised in barren and enriched environments, and transferred between the two environments.

The specific objectives of my study were thus to (1) evaluate the opposing findings that stereotypic animals have either diminished (Mason *et al.* 1995) or increased (Jeppesen *et al*. 2004) fitness, and (2) evaluate the expression of stereotypic behaviours in terms of the coping hypothesis (Rushen 1993), the effects of enrichment (Young 2003), and aspects of perpetuation of the stereotypy as proposed by Mason & Latham (2004) and others.

In order to eliminate the potential effects of long-term housing in captivity on the expression of stereotypy on existing captive populations, the founder population used in this study comprised wild caught individuals. I assumed that the expression of stereotypic behaviours does influence reproductive capacity and that the expression of stereotypic behaviours may have inadvertently or deliberately been selected for in other captive or domestic populations.

I selected the striped mouse for study because it readily breeds in captivity and ample data are available relating to its reproduction and behaviour (Pillay 2000a, b; Schradin & Pillay 2003). *Rhabdomys pumilio* is a common, small (40-60g) southern African rodent. They occur in many different habitat types (Skinner & Smithers 1990), are relatively easy to capture, and readily express stereotypic behaviours in captivity (Schwaibold & Pillay 2001). It is solitary living in the

Highveld grasslands (Schradin & Pillay 2005) from where the individuals used in my study were collected.

1.8 Arrangement of the dissertation

In addition to this introductory chapter, this dissertation comprises three other chapters. Chapters 2 and 3 comprise separate experimental approaches to two distinct aspects of stereotypy. They have been written in a format to facilitate publication and hence some repetition of key concepts and definitions is evident. Chapter 4 discusses the significance of the research undertaken for this study with specific implications for captive animal management.

Chapter 2. Fitness consequences of stereotypic behaviour in the striped mouse *Rhabdomys pumilio*

2.1 Introduction

Stereotypic behaviours are defined as repetitive, invariant acts that appear to lack any goal or function (e.g. Ödberg 1978; Mason 1991a) and, due to their exclusive expression in a wide variety of captive animals, may be considered the outcome of problematic organism-environment interaction (Carlstead 1998). Stereotypies are usually identified because of their qualitatively abnormal or undesirable appearance (Lawrence & Rushen 1993) and are perhaps the most common abnormal behaviour in captive animals (Garner 1999).

There has been a growing body of work on stereotypies, addressing diverse yet complementary issues, such as causal mechanisms (e.g. Schwaibold and Pillay 2001), development (e.g. Ödberg 1987) and function (e.g. Rushen 1993). An aspect that is probably under-represented in the literature is the fitness consequences of stereotypy. One reason for this may be tacit assumption that if welfare is compromised, so too is reproduction (Broom 1983). Another, more theoretical, reason is that it could be deduced that because of the absence of stereotypies in nature, they are considered to have little or no function, negating a need to study fitness.

I am aware of only two studies that have provided a measurable output of the fitness consequences of stereotypy in non-domestic species, both involving farmed mink *Mustela vison*. The results from these studies are equivocal: Mason *et al.* (1995) reported that female mink which display high levels of stereotypic behaviours have young with lower growth rate than females with low levels of stereotypy, whereas Jeppesen *et al*. (2004) reported higher fertility in

stereotypic than non-stereotypic female mink. Notably, in the study by Jeppesen *et al.* (2004), maternal mass was lower in high-stereotypic than low-stereotypic females, alluding to an association between these variables. There are two key considerations for the maintenance of animal populations in captivity; the breeding and welfare of these animals. Exploration of the role of stereotypic behaviours in both of these contexts does require further exploration.

There are two views about the relationship between stereotypy and welfare. The widely accepted view is that the expression of stereotypic behaviours is an indicator of substandard welfare (Broom 1983; Mason 1991a; Mason & Latham 2004; Wiepkema 1987). However, data to verify this conclusively are not available, often because determining the specific causal mechanism of stereotypic behaviour in captive species, and thus any relation to specific welfare concerns, is not always possible (Mason 1991a). The other, less accepted, view is that stereotypies enable animals to cope better with captive environments (Mittleman *et al*. 1991; Rushen 1993). Although some evidence for this coping hypothesis is available (Kennes & de Rycke 1988; Bildsøe *et al*. 1991), the results of other studies do not support the hypothesis (Schouten *et al*. 1991), or have favoured alternative explanations (Würbel & Stauffacher 1997).

In order to better understand the fitness consequences of stereotypic behaviours and their implications for the welfare of captive animals, I compared the reproductive performances of stereotypic and non-stereotypic striped mice *Rhabdomys pumilio*. The striped mouse is a common small (40-60g) southern African rodent, which occurs in many different habitat types (Skinner & Smithers 1990). *Rhabdomys pumilio* breeds readily in captivity, ample data are available about its reproduction and behaviour (Pillay 2000a, b; Schradin & Pillay 2003), and it expresses stereotypic behaviours (Schwaibold & Pillay 2001).

Studies on bank voles *Clethrionomys glareolus* (Schoenecker & Heller 2000) and *R. pumilio* (Schwaibold & Pillay 2001) have provided convincing evidence that stereotypies have a genetic component. Therefore, it is possible that if stereotypic behaviours influence reproductive capacity either negatively or positively, animals displaying stereotypic behaviours may have been inadvertently or deliberately selected for or against in other captive or domestic populations (see also Jeppesen *et al*. 2004). To overcome the potential effects of such selection, the founder population used in this study comprised wild caught individuals, and I assumed that the potential selective pressures for or against stereotypic behaviours were negligible in my experiments.

In this study, breeding pairs were established in which both parents were either stereotypic or non-stereotypic, and in which one of the parents was stereotypic. This protocol provided the opportunity not only to test the influence of genetic transmission of stereotypy in *R. pumilio* but also to evaluate the contributions of one or both parents to stereotypic behaviour, since the relationship between the captive environment and genetic predisposition on the expression of stereotypic behaviours is still unclear (Schwaibold & Pillay 2001; Jeppesen *et al*. 2004). Several reproductive parameters were measured, including reproductive output, maternal investment, and offspring growth and development. I tested the null hypothesis that the reproductive performance of stereotypic or non-stereotypic striped mice would be similar.

2.2 1 Materials and Methods

A founder population of 62 wild-caught adult striped mice *R. pumilio* was obtained from Cullinan ($25^0$40''S; $28^0$30'E), South Africa. The animals were housed at the Milner Park Animal Unit at the University of the Witwatersrand, Johannesburg, in a room with partial environmental control (light regime of 14L: 10D, 20 to 24°C, 30-60% rH) in 400x250x120 mm Lab-o-tec cages.

They were fed Epol^{R} commercial mouse cubes and water was provided *ad libitum*. The diet was supplemented with a parrot food mix of various seeds twice a week. For an initial three week acclimatisation period, the mice were housed singly in standard laboratory cages, and supplied with coarse wood shavings for bedding and hay for cover.

Following the acclimatisation period, individuals were transferred into "barren" Lab-o-tec cages to elicit stereotypic behaviours (*cf* Cooper *et al*. 1996). These cages were identical to those described above except that no hay was provided for cover. Individuals were maintained in these conditions for a period of two months. Thereafter, their behaviour was video-recorded to identify which animals exhibited stereotypic behaviours.

Video-recordings were made between 08h00 and 13h00 every second day for 10 days; *R. pumilio* is diurnal and most active in the mornings (Pillay 2000a). No human observers were present in the room during taping. Animals which displayed stereotypies consistently (>60% of observation sessions) were regarded as stereotypers, whereas those that displayed no stereotypy were classified as non-stereotypers.

Twenty-three of the 62 animals were stereotypers. Twenty stereotypers (10 of each sex) and 20 non-stereotypers (10 of each sex) were randomly paired. In order to minimise bias due to prior familiarity and kinship, pairs comprised animals that did not meet in captivity previously and which were unlikely to have made contact in the wild because they were trapped in different widely-spaced (>250m) trap lines. These pairings were housed in enriched conditions (i.e. cages contained wood shavings, wood wool, hay for bedding, 10 cm long, 4mm diameter, dowel chew sticks and a plastic commercially available mouse house). The F1 offspring produced were separated from their parents at weaning (20 days old) and housed in same-sex kin groups until they were sexually mature (i.e. 80 days old). During this time, their behaviour was video-

recorded as described above to determine stereotypers and non-stereotypers. F1 individuals were used for the breeding experiment as this population provided a large sample size where the age and breeding status of the animal was known, as well as the time when stereotypic behaviours developed. These animals were then paired, by randomly assigning them to one of four treatments, based on combinations of stereotypy and non-stereotypy: (1) non -stereotypic female paired with non-stereotypic male (NS-NS); (2) non-stereotypic female paired with stereotypic male (NS-S); (3) stereotypic female paired with non-stereotypic male (S-NS); and (4) stereotypic female paired with stereotypic male (S-S). Males and females in pairs were unrelated and did not make prior contact.

Pairs were held together for 100 days or until the birth of the third litter, whichever occurred earlier. The number of successful pairs in each treatment was recorded, and the following was recorded for successful pairs: interval between pairing and birth of the first litter, inter-litter interval, number of litters and litter size. Litters and the mother were weighed on the day of birth (day 0) and again on day 20, and the pre-weaning growth rates of litters was calculated using the formula [ln (mass time 1) – ln (mass time 2)]/(time 2 – time 1); the growth rate of litters rather than individuals was considered since offspring in a related group are not statistically independent of each other (Boonstra & Hochachka 1997). The sex ratio of litters was ascertained at birth, and the proportion of offspring in a litter that survived to weaning was recorded. At weaning, the expression of stereotypic behaviours in the offspring was also noted.

2.2.2 Data analysis

Before using parametric tests, I tested data sets for departure from normality and for homogenous variances (Zar 1996). Non-parametric statistics were used to compare the following

parameters among the treatments: numbers of pairs reproducing (chi-square); sex ratio (heterogeneity chi-square); percentage offspring surviving to weaning and growth rate (Kruskal-Wallis Anova); and proportion of stereotypic offspring (Fisher's exact test). General linear models (GLM) were used to compare other parameters across treatments, including interval between paring and production of the first litter, inter litter interval, maternal mass, litter size (maternal mass included as a co-variate), and total number of young per pair. In addition to growth rate, I also compared changes in litter mass from day 0 to day 20 using a repeated measures design. Tukey HSD post-hoc tests were used to identify specific trends when probabilities in the GLM analyses were significant at $\alpha \leq 0.05$. All tests were two-tailed.

2.3 Results

The number of reproducing pairs was lowest in the NS-S treatment (66%) and highest in the S-NS and S-S (93%) treatments (Table 2.1). However, these proportions were not significantly different, possibly because of the small sample size (power of this test was $\beta=0.572$). Pairs in the S-S treatment produced their first litters quicker than other pairs, and significantly faster than those of the NS-S treatment. There was no statistical differences across treatments in the inter litter interval, maternal mass and the number of litters produced by each pair (Table 2.1).

Table 2.2 shows the litter characteristics of successful pairings. Litter size was significantly larger in treatments in which the female (S-NS) or both parents (S-S) were stereotypic. Importantly, maternal mass was not a good predictor of litter size ($F_{1,104}=0.234$, $P=0.630$; GLM with maternal mass as a co-variate). The pattern observed for the total number of young per pair and offspring survival were similar to that of litter size (i.e. greater in S-NS and S-S vs NS-S and NS-NS).

Table 2.1. Reproductive performance of four *R. pumilio* breeding treatments. Except for number of pairs reproducing, all data provided as mean (±SE). NS = non-stereotypic; S = stereotypic. Specific differences are provided for significant statistics.

Reproductive parameters	NS-NS	S-NS	NS-S	S-S	Statistics	Specific differences
No. of pairs reproducing/total pairs	12/15	14/15	10/15	14/15	$\chi^2_3 = 0.49$; P=0.920	
Pairing to first litter	32.00 (2.86)	30.00 (2.54)	38.27 (4.09)	27.21 (1.08)	$F_{3,47}=2.92$, P=0.043	S-S < NS-S
Inter litter interval	27.25 (1.47)	25.00 (0.54)	28.00 (2.19)	27.00 (0.92)	$F_{3,76}=1.47$, P=0.227	
Maternal mass	59.59 (4.68)	69.00 (2.91)	71.80 (3.71)	71.50 (2.75)	$F_{1,104}=0.23$, P=0.630	
Litters per pair	1.80 (0.35)	2.47 (0.26)	1.80 (0.40)	2.60 (0.24)	$F_{3,55}=0.91$, P=0.441	

Table 2.2. Mean (±SE) litter size, total offspring produced and survival of offspring produced by the four breeding treatments of *R. pumilio*. NS = non-stereotypic; S = stereotypic

Litter characteristics	NS-NS	S-NS	NS-S	S-S	Statistics	Specific differences
Litter size	4.56 (0.39)	6.86 (0.27)	4.48 (0.31)	7.51 (0.29)	$F_{3,104}=27.15$, P<0.001	S-NS=S-S > NS-S=NS-NS
Total number of young per pair	8.20 (1.96)	16.00 (2.19)	8.07 (1.82)	19.53 (2.23)	$F_{3,56}=9.04$, P<0.001	S-NS=S-S > NS-S=NS-NS
Offspring survival (%)	84.70 (3.87)	98.68 (0.81)	96.06 (2.49)	98.67 (0.87)	$H_{3,128}=17.62$, P<0.001	S-S=S-NS > NS-S=NS-NS

The sex ratio of the offspring did not differ significantly from parity in any of the four treatments: NS-NS (87: 82 female: male, $\chi^2_{13} = 8.62$; P=0.806); S-NS (120: 117, $\chi^2_{13} = 4.87$; P=0.978); NS-S (77: 79, $\chi^2_{12} = 4.39$; P=0.975) and S-S (155:158, $\chi^2_{14} = 3.72$; P=0.997)

After statistically accounting for litter size, litters in the S-S and S-NS treatments were heavier than their counterparts in the NS-S and NS-NS treatments (Table 2.3). Despite these differences in litter mass, the rate at which litters gained weight (growth rate) was not statistically different across treatments.

Table 2.3. Mean (±SE) growth parameters of litters resulting from four breeding treatments of *R. pumilio*. Litter mass values are adjusted for litter size on days 0 and 20 respectively. NS = non-stereotypic; S = stereotypic. Specific differences are provided for significant statistics.

Growth parameters	NS-NS	S-NS	NS-S	S-S	Statistics	Specific differences
Litter mass day 0 (g)	3.25 (0.13)	3.39 (0.073)	3.13 (0.07)	3.37 (0.06)	$F_{1,305}$=91.05, P<0.001	S-S=S-NS > NS-S=NS-NS
Litter mass day 20 (g)	10.35 (0.85)	21.27 (0.54)	13.82 (0.50)	21.92 (0.48)		
Growth rate (g/day)	0.016 (0.001)	0.018 (0.001)	0.018 (0.002)	0.018 (0.002)	$H_{3,110}$=4.47, P=0.192	

There was no difference in the numbers of females and males in each treatment that displayed stereotypy (Table 2.4). However, there was a graded response in the number of offspring within each treatment that displayed stereotypic behaviours, decreasing significantly from S-S and S-NS pairs to NS-S pairs to NS-NS pairs (Figure 2.1).

Table 2.4. Proportion of female and male stereotypic offspring produced by four *R. pumilio* treatments. NS = non-stereotypic; S = stereotypic.

Parameters	NS-NS	S-NS	NS-S	S-S
Stereotypic females/total females	7/87	64/120	21/77	90/155
Stereotypic males/total males	5/82	63/117	17/79	67/158
Fisher statistics	P=0.769	P=1.000	P=0.589	P=0.118

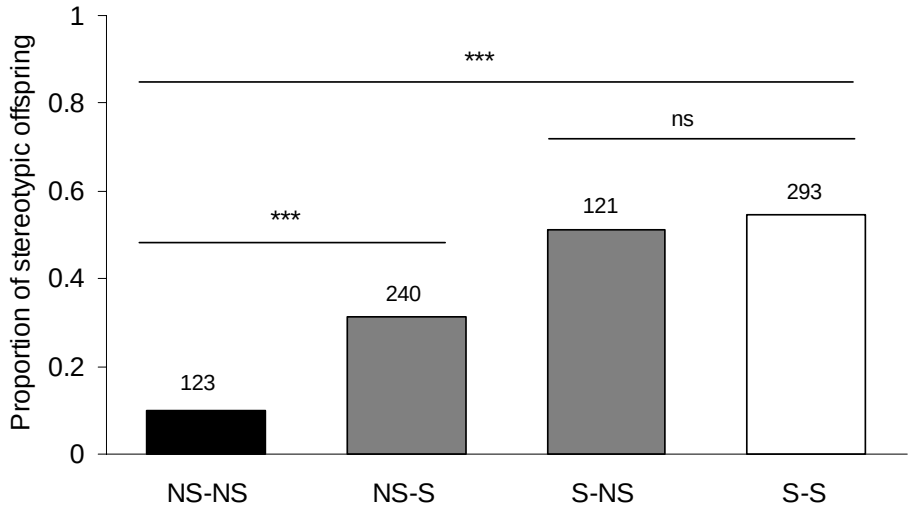

Figure 2.1. Proportion of stereotypic offspring in four *R. pumilio* treatments. NS = non-stereotypic; S = stereotypic. Sample sizes are shown. ns = $p>0.05$, ***: $p<0.001$.

2.4 Discussion

The reproductive performance of *R. pumilio* in the present study depended on whether or not the female was stereotypic. Treatments in which the mother was stereotypic (S-S and S-NS) produced the first litter (interval between pairing and the first litter) quicker and produced more offspring than treatments in which the mother (NS-S) and both parents (NS-NS) were non-stereotypic. There was no significant difference in the reproductive performance of pairs in which both parents were stereotypic compared to when only the mother was stereotypic.

The positive relationship between stereotypy and reproductive success observed here was also reported in farmed mink *M. vison* by Jeppesen *et al*. (2004). Mason *et al*. (1995) found a slower growth rate in high-stereotypic mink, which indicates a negative effect on fitness. Jeppesen *et al.* (2004) maintaind that the relationship between body mass and fertility is an epiphenomenon, concluding that the increased activity of stereotypic females results in low body mass which in turn promotes better physical condition and increased fertility. In contrast, Mason

et al. (1995) maintained that since stereotypic animals have an inherent need to stereotypy, they display higher activity, have lower body mass, and do not adequately nurture their young, specifically because of inadequate nest building behaviour. I reported in another study that stereotypic *R. pumilio* displayed higher levels of activity than non-stereotypic striped mice (Chapter 3) but surprisingly this did not influence body mass of females in the present study. Therefore, my results do not show a similar relationship between activity, body mass and reproduction. I did not specifically measure maternal care, but even if it was poorer in stereotypic mice, it did not negatively influence offspring.

While the causal mechanism underlying the better reproduction of stereotypic females is not apparent in my study, it is notable that the reproductive success of non-stereotypic females paired with stereotypic males (NS-S) was similar in almost all respects to the NS-NS treatment. It is clear that the higher reproductive success of S-S and S-NS treatments is due mostly to the role of the stereotypic female.

My data suggest that stereotypy is genetically transmitted, since the incidence of stereotypy was 3-4 times more common in the offspring of stereotypic than non-stereotypic females. Similar findings were reported in another study of *R. pumilio* (Schwaibold & Pillay 2001) and in studies of *C. glareolus* (Schoenecker & Heller 2000) and *M. vison* (Jeppesen *et al*. 2004). However, I cannot rule out non-genetic factors. The genetic contribution of the male may explain the incidence of stereotypy in offspring in the NS-S treatment but not in the NS-NS treatment. Moreover, the proportion of stereotypic offspring in the S-NS treatment was significantly greater than in the NS-S treatment (i.e. when one of the parents was stereotypic), and it seems plausible to assume that the presence of a stereotypic mother adds to transmission of this behaviour.

Like the transmission of stereotypy, the better reproductive output of stereotypic females is likely to be a combination of genetic and environmental factors, since S-NS pairs had greater fitness than NS-S pairs. In mink, stereotypy appeared to improve female condition (Jeppensen *et al*. 2004), but I could not detect a similar occurrence in my study. Clearly, future studies should investigate the association between genetic predisposition and environmental circumstances on the transmission of stereotypy.

Stereotypies are often regarded as a sign of poor welfare (Mason 1991b) but another view is that animals which express stereotypic behaviours are better able to cope with the stresses of living in a captive environment (Rushen 1993). Thus, it can be assumed that animals that can cope better are likely to have a higher fitness. Stereotypic female *R. pumilio* had higher fitness than non-stereotypic females, both in terms of reproductive output and offspring survival, indicating that the welfare of stereotypic *R. pumilio* is not compromised and that they cope with captive conditions. However, coping with captive conditions does not necessarily imply that the welfare needs of an animal have been met (Kanis *et al*. 2004).

In conclusion, stereotypy positively influences the fitness of *R. pumilio*, particularly if the female is stereotypic. Although the mechanism promoting increased fertility of stereotypic females is not known, it is likely that a combination of genetic and environmental factors is involved. In addition, Jeppesen *et al*. (2004) propose that the relationship between stereotypy and fitness of other species is not linear but part of a more complex phenotypic expression, which would be supported by our conclusions.

Chapter 3. The expression of stereotypic behaviour in striped mice raised in barren and enriched environments

3.1 Introduction

Stereotypic behaviour has been associated with problematic organism-environment interaction (Carlstead 1998), and viewed as an indicator of poor or sub-standard welfare (Wiepkema 1987; Broom 1983; Mason 1991a; Mason & Latham 2004). Confirmation of this view is that the frequency of expression of stereotypic behaviours is much greater in animals housed in sub-standard environments (Shepherdson 1998, Mason 1991). While stereotypies may reflect psychological and physiological stress, another view is that stereotypic animals cope better with poor conditions, which is referred to as the coping hypothesis (Rushen 1993).

The copying hypothesis has not received wide support, possibly because of a lack of identified functions for stereotypy, but this may reflect our current state of knowledge, rather than an intrinsic property of the behaviour (Duncan *et al*., 1993). Therefore, we cannot assume *de facto* that stereotypic behaviour reflects poor welfare. Moreover, Mason and Latham (2004) advise that stereotypies should always be taken as a warning of potential suffering but are not necessarily a conclusive indicator as such.

Another difficulty with relating stereotypies with poor welfare is that the performance of a stereotypy may be unrelated to the original causes (Cooper & Nicol 1996), particularly if the behaviour is incorporated into the repertoire of an animal (Duncan & Wood-Gush 1972) and perseveres in a range of different environments. For example, transferring bank voles *Clethrionomys glareolus* from barren to enriched cages reduces the incidence of stereotypies, but is less effective in older animals (Cooper & Nicol 1996). Stereotypies become perseverative (or

bad habits) if they become centrally controlled (Mason and Latham 2004) and unresponsive to particular cues in the environment (Fentress 1973). Alternately, the stereotypic behaviour may become self- reinforcing (Dantzer 1986; Mason & Latham 2004). Thus, the current expression of stereotypy may be indicative of previous welfare problems and are most probably unreliable indicators of the animal's current welfare.

Nonetheless, the welfare of captive animals remains a priority and once psychological and/or physiological suffering have been identified, several remedial actions can be implemented (see Dawkins 1983; Maple 1998). Environmental enrichment has been one of the more successful programmes employed, since it has provided a system in which interventions applied to captive animals can be objectively designed, implemented, and assessed (Shepherdson *et al*. 1998; Young 2003). Although other methods have been investigated for controlling stereotypies (see Tarou *et al.* 2003; Poulsen *et al.* 1996), enrichment remains the primary tool for controlling stereotypies, as well as other perceived adverse behaviours (Young, 2003).

Some environmental enrichments have successfully reduced rates of stereotypy (Carlstead 1998), or potentially prevented their development, but this success is often fortuitous rather than a predetermined outcome, and many enrichment attempts have been unsuccessful (Shepherdson *et al.* 1998). Ironically, due to the uncertain nature of stereotypy expression, and allusions to underlying genetic bases for its expression, it is difficult to categorically confirm the role of enrichment in limiting the expression of stereotypic behaviours in the first place.

The aim of the present study was to use an environmental enrichment procedure to investigate the persistence of stereotypies through time in striped mice *Rhabdomys pumilio*. Striped mice are small (40g) African murid rodents which readily display stereotypies in captivity (Schwaibold & Pillay 2001). Using a protocol developed by Cooper & Nicol (1996), I first

identified stereotypic and non-stereotypic striped mice and housed them singly in barren or enriched cages and two months later swapped between cage types. I tested three predictions. 1) Stereotypic striped mice raised in a barren environment will display higher levels of stereotypic behaviours than those raised in an enriched environment. 2) Stereotypic striped mice that have been raised in a barren environment will show reduced stereotypies when transferred to an enriched environment if the behaviour is not a 'bad habit' and will alternatively show no reduction in expression of stereotypies if the behaviour has become a 'bad habit'. 3) Stereotypic striped mice raised in an enriched environment will show increased frequencies of stereotypic behaviours when transferred to a barren environment.

3.2.1 Methods and Materials

Second generation captive bred striped mice *Rhabdomys pumilio* were used in this study. These were the offspring of F1 pairings described in Chapter 2 that were separated from their parents on day 20 and housed in same-sex kin groups. Their behaviour was video-recorded to establish whether or not they were stereotypers (see Chapter 2). On day 25, 40 striped mice (20 stereotypers and 20 non-stereotypers) from different litters were transferred into enriched cages (wood shavings; wood wool; hay for bedding; one 10 cm long, 4mm diameter, dowel chew stick and a plastic commercially available mouse house) and 40 striped mice (20 stereotypers and 20 non-stereotypers) were transferred into barren cages (standard laboratory cages with only wood shaving substrate). The striped mice were housed singly and the sexes were equally represented in both treatments. After 60 days, the behaviour of all individuals was video-recorded in two sessions over two days for 15 min per day. Thereafter, they swapped between treatments (i.e. transferred from barren to enriched cages and vice versa). After another 60 days (i.e.

approximately 120 days), the behaviour of individuals was again video-recorded for two days as described above.

Using continuous focal sampling, the frequency of the following behaviours were recorded for each time period : inactive (no locomotion or out of view in the nest); explore (walking and running around the cage, sometimes marking without any repetition); feeding and drinking (upright standing at the food trough and gnawing at pellets or gnawing at a piece of pellet held between the paws, drinking water); digging (mouse digging in woodshavings); manipulating (handling hay, cage additions); grooming (self-grooming); and stereotypy. All observations were recorded using the Observer software (version 5.0 for Windows; Noldus Information Technology) on a personal computer. The data for each striped mouse were converted to percentages over the two days of observations in each time period.

3.2.2 Data analysis

The data set was arcsin transformed to approximate normality and the behaviours in the first and second housing conditions were compared using a general linear model (GLM) for multiple dependents with a repeated measures design. Separate analyses were conducted for stereotypic and non-stereotypic striped mice because non-stereotypic animals never displayed stereotypy. In the GLM, the transfer protocol was the independent factor, and behaviours during initial and final housing conditions were the dependent factors. Data for the sexes were pooled because behaviour was not influenced by sex. Tukey HSD post-hoc tests were used to identify specific trends when GLM probabilities were significant at $\alpha \leq 0.05$.

3.3 Results

Transferring striped mice from barren to enriched cages and vice versa had a greater affect on stereotypic than non-stereotypic individuals. For stereotypic animals, the type of transfer significantly influenced behaviour ($F_{6, 33} = 4.8$, $p = 0.001$), with inactivity increasing and stereotypy decreasing in enriched cages (post hoc tests). The time of sampling (i.e. the repeated measures variable) did not significantly influence behaviours. However, the statistical interaction between transfer and time was significant ($F_{6, 33} = 3.5$, $p = 0.009$). In this study, this interaction provides a statistical measure of the effects of the enrichment. Post hoc tests revealed that individuals in barren cages were significantly less active than those in enriched cages, and that inactivity increased significantly when individuals were transferred from barren to enriched cages and decreased significantly when individuals were transferred from enriched to barren cages (Figure 3.1). Importantly, levels of stereotypy were highest when animals were raised to 60 days of age in a barren cage and decreased significantly when these individuals were transferred to enriched cages (Figure 3.1a). Stereotypy was not completely disrupted, however, and only two of the 20 stereotypic individuals did not show stereotypy during observations when transferred from barren to enriched cages. None of stereotypic individuals raised in enriched cages stopped stereotypy when transferred to barren cages and there were no significant increases in stereotypy (Figure 3.1b) and levels matched those of striped mice transferred from barren to enriched cages (Figure 3.1a). Levels of exploratory behaviour did not change between treatments.

Neither inactive nor exploratory behaviour changed significantly when non-stereotypic striped mice where transferred between barren and enriched cages (Figure 3.2a) or from enriched to barren cages (Figure 3.2b).

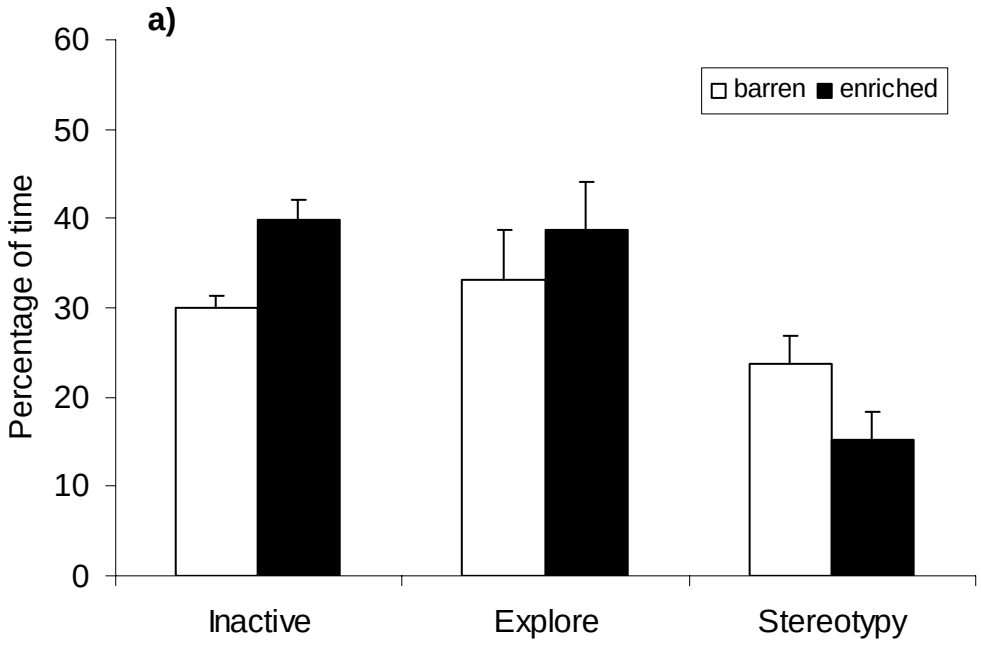

Figure 3.1a. Mean (± SE) percentage of inactive, exploratory and stereotypic behaviour in stereotyping *R. pumilio* transferred from a barren to an enriched environment.

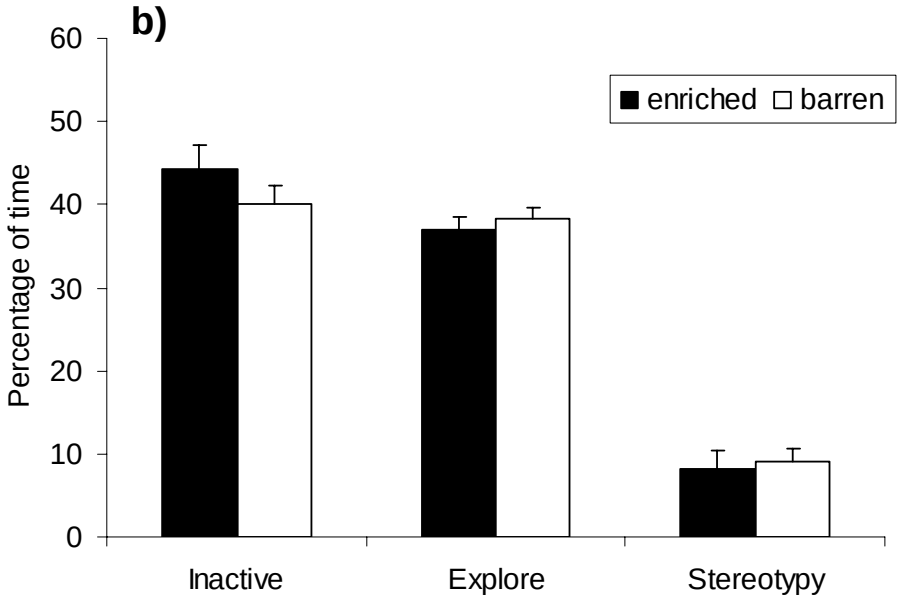

Figure 3.1b. Mean (± SE) percentage of inactive, exploratory and stereotypic behaviour in stereotyping *R. pumilio* transferred from an enriched to a barren environment.

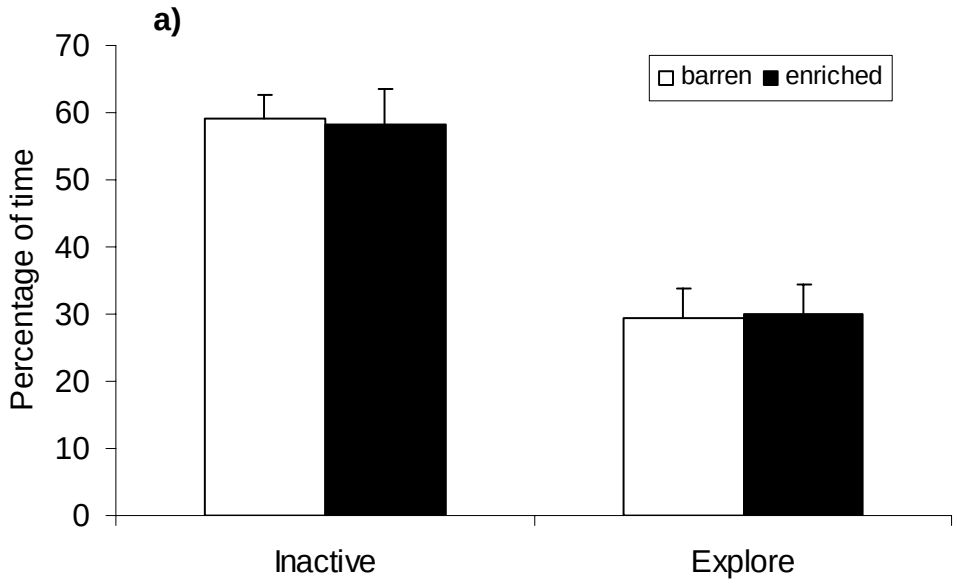

Figure 3.2a. Mean (± SE) percentage of inactive and exploratory behaviour in non-stereotyping *R. pumilio* transferred from a barren to an enriched environment.

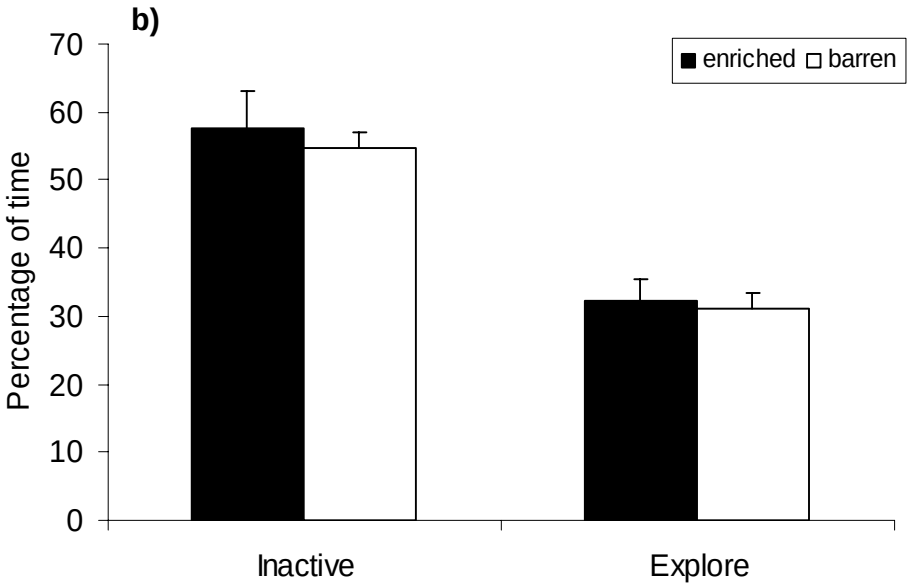

Figure 3.2b. Mean (± SE) percentage of inactive and exploratory behaviour in non-stereotyping *R. pumilio* transferred from an enriched to a barren environment.

The other behaviours I scored occurred at very low levels, and were not statistically influenced by the changes in housing conditions. These data are summarised in Table 3.1.

3.4 Discussion

Based on the predictions tested in this study, three trends emerged. Firstly, stereotypic striped mice raised in a barren environment displayed higher levels of stereotypic behaviours than those raised in an enriched environment. Secondly, striped mice transferred from barren to enriched cages showed a significant decrease in stereotypic behaviours. Thirdly, the incidence of stereotypy did not increase when striped mice where transferred from barren into enriched cages.

This study demonstrated that while there was a measurable variance in the expression of stereotypy under enriched conditions, these behaviours became perseverant and harder to disrupt in older animals transferred from barren to enriched cages. The perseverance of stereotypic behaviour is well known (Mason 1991a; Garner & Mason 2002), and has been experimentally demonstrated in bank voles *C. glareolus* (Cooper & Nicol 1996). Many hypotheses have been erected to interpret why perseveration occurs, including bad habit formation (Hinde 1970; Fentress 1976; Mason & Turner 1993) channelling (the narrowing of a behavioural repertoire to a few key behaviours due to environment; Lawrence & Terlouw 1993) and lack of behavioural competition (Hinde 1962; Mason and Turner 1993), which may lead to specific brain abnormalities (Garner & Mason 2002). This research does not expound on any of these specific behaviours and I aimed to investigate the concept of perseveration rather than the mechanism by which it occurs.

Table 3.1. Mean (±SE) percentage of four behaviours for stereotypy and non-stereotypy *R. pumilio* transferred from barren to enriched cages and from enriched to barren cages.

	Barren to enriched				**Enriched to barren**			
	Stereotypy		**Non-stereotypy**		**Stereotypy**		**Non-stereotypy**	
Behaviour	**Barren**	**Enriched**	**Barren**	**Enriched**	**Enriched**	**Barren**	**Enriched**	**Barren**
Feed and drink	4.39 (0.39)	4.38 (0.60)	3.97 (0.44)	3.53 (0.51)	4.27 (0.46)	3.90 (0.57)	3.75 (0.38)	4.40 (0.46)
Digging	2.97 (0.30)	4.74 (0.58)	3.42 (0.40)	4.19 (0.51)	2.54 (0.43)	4.37 (0.55)	3.21 (0.40)	5.02 (0.52)
Manipulating	2.74 (0.39)	3.82 (0.56)	3.90 (0.34)	4.62 (0.59)	3.76 (0.47)	4.19 (0.31)	3.27 (0.43)	4.80 (0.56)
Grooming	3.24 (0.12)	2.15 (0.23)	2.23 (1.23)	3.44 (0.43)	6.33 (1.83)	3.19 (0.23)	4.33 (0.44)	3.45 (0.43)

Similarly animals that were transferred from an enriched environment to a barren environment did not develop stereotypies and although this does not concur with the coping hypothesis necessarily (Rushen 1993), I feel that these animals may too have developed perseverative behaviours that had become entrenched in these older individuals that prevent the development or heightened expression of stereotypies. Schwaibold and Pillay (2001) did indicate that the expression of stereotypic behaviour in striped mice is genetically transmitted and a specific lack of genetic predisposition to development of stereotypies may too have affected this lack of phenotypic expression.

Compared to non-stereotypic striped mice, stereotypic striped mice were more active (lower levels of inactivity). Interestingly, levels of activity in stereotypic striped mice tracked the transferring protocol, decreasing from barren to enriched cages and increasing from enriched to barren cages. This association between high levels of activity and stereotypies was also reported in studies of laboratory mice (Würbel *et al.* 1998) and bank voles (Cooper & Nicol 1996) but not in other studies of bank voles (Ödberg 1986, 1987). The decrease in stereotypies coupled with an increase in inactivity possibly represents similar behavioural organisation (Cooper & Nicol 1996) or motivation (Würbel *et al.* 1998) in response to changes in environmental conditions, but I cannot separate out the age effects on this behaviour in this study.

Schoeneker *et al.* (2000) reported the development of polydipsia in bank voles in relation to housing in impoverished environments and related this as a possible physiological response to the inadequate captive environment, either in conjunction with, or without the expression of stereotypies. In this study, which is of similar design, no change in drinking rates was observed, although stereotypies were present. This could be attributed to specific biological differences between bank voles and striped mice.

Stereotypic striped mice housed initially in enriched environments displayed comparatively low levels of stereotypy which did not increase when they were transferred to barren cages. Clearly, it is more appropriate to ensure that enrichment is implemented from an early age, rather than later on where it is likely to be less successful. Such conclusions have implications for the welfare of these animals. The benefits of enrichment for persistently stereotyping animals have yet to be explored, although behavioural choice experiments have indicated that stereotyping bank voles find barren environments less aversive than non-stereotyping bank voles (Cooper & Nicol 1991). This does pose an interesting situation where the addition of excessive enrichment may prevent the animal from exhibiting stereotypy, and thus may be contrary to the best welfare practice for that specific individual. Unfortunately, it appears that this reactive approach is far more common in captive animals (particularly in zoos) where enrichment tends to become increasingly important only after the development of undesirable behaviours (Young 2003).

Enrichment has shown to be a successful mechanism for preventing stereotypies in animals displaying these behaviours for some time, particularly when the right form of enrichment has been targeted at the correct stereotypy (Carlstead 1998; Shepherdson *et al.* 1998) For example, entrenched crib biting behaviour in horses over extended periods of time can be halted through appropriate changes in diet (Baxter & Plowman 2001). In this case, no perseveration was noted. In my study, enriched cages did not stop stereotypy, indicating that the stereotypic behaviour are likely to have become perseverative, but may also mean that the appropriate environmental enrichment protocols were not applied (see Kaufman *et al.* 2004). Nevertheless, there was a significant decrease in the levels of stereotypy in striped mice

transferred into enriched cages. Further studies are required to investigate how cage design can be manipulated to influence stereotypy.

In conclusion the enrichment protocol implemented was effective in preventing the development of stereotypic behaviours in enriched cages which would substantiate the coping hypothesis (Rushen 1993). The lack of effectiveness in substantially reducing or eliminating the stereotypic behaviours in animals raised in barren environments and transferred to enriched cages supports the concept of perseveration, although the exact mechanism thereof remains uncertain. In terms of the coping hypothesis, the failure of non-stereotyping animals to develop stereotypies when transferred to the barren environment is indicative that (1) through some perseverative mechanism the adult animal was unable to develop stereotypies and maintained its behavioural repertoire from an enriched to a barren environment, or (2) it lacked the genetic predisposition to perform this behaviour.

Chapter 4. General Discussion

This research set out to investigate some key aspects of stereotypic behaviour. It is evident from the literature presented in this document that there is a plethora of information available on stereotypic behaviours relating to the causation, development and function of stereotypies in laboratory, domestic and zoo stock (e.g. Mason 1991a; Young 2003). However much of this information is contradictory, and often flawed in both experimental design and interpretation.

The coping hypothesis proposed by Rushen (1993) remains a plausible but not widely accepted explanation for the expression of stereotypies, through mechanisms such as self-narcotisation (Cronin et al. 1985) and attenuating the effects of physical stress (Dantzer, 1991). Another less popular view is the pathology hypothesis (see Garner 1999) through mechanisms such as behavioural sensitisation (Dantzer 1986) and channelling (Hinde 1970). It is likely that the difficulty in ascertaining both which hypothesis is valid, and determining the mechanism through which the hypothesis applies to stereotypy, is due to the diversity both in terms of form of expression, and diversity of species expression (Mason 1991a).

My study had two main objectives: 1) to investigate fitness of stereotyping vs. non-stereotyping striped mice in terms of the coping hypothesis; and 2) to investigate the concepts of perseveration of stereotypies and the affects of enriched and barren cages on the expression of stereotypies.

My findings from experiment 1 concur with those by Jeppesen *et al.* (2004) in that the stereotypic animals had better reproductive output. I did not, however, record a difference in the mass of stereotyping and non-stereotyping female striped mice, as was found by Jeppesen *et al.* (2004). In this study with mink the authors found that stereotypic mink weighed less, and this

was taken as an indication that it was not the performance of stereotypic behaviours *per se*, but rather that stereotyping mink were less obese than their non-stereotypic counterparts, that resulted in their findings. I thus conclude that these results substantiate the coping hypothesis (Rushen 1993), since stereotyping animals had a higher fitness and thus appear to cope better in the captive environment when compared to non-stereotypic striped mice. I found that there was a difference between stereotypic and non-stereotypic pair combinations, with pairs with stereotypic females performing best. Those pairs with stereotyping fathers, or no stereotyping performed worst, which is supportive of both a genetic effect (demonstrated previously in this species by Schwaibold and Pillay 2001) and maternal effects (Boonstra Hochachka 1997). This model of individual-environment interaction has been termed the diathesis-stress model, and is the accepted model for the development of most, if not all, mental illness in humans (Barlow & Durand 1999), indicating that many human-developed models may well apply to other animal species.

Obtaining a valid and effective measure of the fitness consequences of stereotypy and their effects on population dynamics requires a study population unaffected by prolonged artificial selective pressure in captivity. It remains unclear if there are a number of types of stereotypy (Mason 1993b), or through what pathways these stereotypies arise, particularly with regards to coping (for instance see Mason 1991; Rushen 1993). Although the expression of stereotypy is a captive phenomenon, an underlying mechanism that exists in some form in wild animals must be present to result in the phenotypic expression of the stereotypic behaviours. In order to investigate this specific phenomenon, in terms of effects of fitness and what is likely to affect all captive stereotypic populations, I felt that the use of wild caught animals was imperative,

particularly if the form of coping in captivity through stereotypy expression further advances our understanding of striped mouse behaviour.

Nesse (1999) explores the concept of stress in an evolutionary context in that an organisms ability or inability to cope with stress is a fundamental aspect of its potential for survival. He argues that understanding stress (and anxiety) in an evolutionary context will allow for the creation of a conceptual framework to better understand the concept of stress and dealing with this stress. In exploring coping with stressful events, Koolhaas *et al.* (1999) refer to different coping strategies in a broad biological context, which are either proactive or reactive in type. They emphasise that the concept of coping is a multifaceted strategy that is based on genetic predisposition and environmental factors. In striped mice, it is evident that those rodents that express stereotypic behaviours exhibit a proactive coping strategy. In line with the hypothesis of Koolhaas *et al.* (1999), those striped mice that do not express stereotypies are exhibiting a reactive coping strategy of some type, one that from a reproductive perspective has, in this study, been shown to be less effective.

My data indicate that it is likely, at least in striped mice, that as the stereotyping individuals had a higher reproductive output, through time the population will naturally be biased towards this behaviour and in a random breeding system, unless the expression of stereotypic behaviours is actively selected against, the expression of stereotypy will increase in the population.

The results of the enrichment experiments supported the hypotheses of Clubb and Mason (2003) and experiments by others (e.g. Cooper & Nicol 1996) that stereotypy in striped mice appears to have become perseverative and independent of the original stimulus, as indicated by the lack of a substantial response to enrichment by stereotyping striped mice. Factors influencing the development of a behaviour, such as stereotypy, include an animal's genetic predisposition,

the influences of the environment during its ontogeny (West-Eberhard, 2003), and the cumulative effects of the outcomes of prior interactions between the animal's environment and its genome (Koolhaas *et al.* 1999). I did not set out to investigate the mechanism of perseveration but rather to explore the concept of perseveration of stereotypic behaviours in terms of the effects of enriched and barren environments on the expression of stereotypic behaviours and relate this to the coping hypothesis. My data, at first surprisingly, indicated that animals moved from an enriched to a barren environment did not develop stereotypies. However, if perseveration is a factor that prevents the effectiveness of enrichment on reduction of stereotypy in adult animals moving from a barren to enriched environment, the same or a similar mechanism may well operate in limiting the possibility of an animal developing stereotypies when the converse is true. This would imply that some mechanisms discussed in perseveration theories might apply to a behavioural repertoire in general, which can include or exclude stereotypic behaviours.

Stereotypy is frequently perceived as an indicator of poor welfare. It has, however, been demonstrated that stereotypy cannot be viewed in isolation and must form part of an integral assessment of welfare (Mason 1991b; Mason & Latham 2004). The results of my experimental approach indicate that, depending on the circumstances of the individual, the expression of stereotypy is a potential sign of positive welfare. It may actually be worthwhile to specifically elicit stereotypic behaviours in order to improve the welfare, and in certain cases, breeding success, of captive animals that are housed in environments that cannot be improved dramatically through extensive enrichment techniques. Through the concept of perseveration, I conclude that from a welfare perspective, effort should be applied to combating stereotypies before they arise, rather than attempting to eliminate them once they have actually developed. However, it must be questioned whether the opinion of stereotypic behaviours in captivity is not often tainted by our

perceived lack of desirability of stereotypies and hence our objectivity in assessing them is inherently biased. Stereotyping striped mice certainly do better.

My study has added to the knowledge of the captive management of animals. The implications for the management of captive animals based on the increased breeding success of stereotyping individuals are obvious. However, I do caution that this study was based on a species which produces many offspring very rapidly (i.e. r-strategists; Pianka 1970), and did focus on a single population of a single species. In order to conclusively investigate the affects of enrichment, and the relationship between enrichment and stereotypy, I would recommend that further studies be undertaken, in a similar experimental design, but comparing the fitness of striped mice housed in barren and enriched environments. This will identify whether enrichment is effective in reducing the need for coping. I would predict that even with extensive enrichments, certain fundamental biological needs will still be thwarted in some way and it is likely that those animals that persist in the performance of stereotypies, will in fact, still cope better and demonstrate a higher fitness. Remignon *et al.* (1998) showed that Japanese quail (*Coturnix japonica*) that exhibited a perceived desirable behavioural phenotype (in this case lack of expression of fear) were in fact animals that showed exceptionally high physiological levels of stress. In a similar way the selection of animals that do or do not show stereotypic behaviour may be similar to this and this too would be worth investigating further.

The concept of behavioural perseveration indicates that the rearing environment of animals needs to carefully considered. My research does not explore the long term consequences of stereotypy expression, including generational effects and longevity (Margulis 1998).

The fitness benefits of animals that do express stereotypic behaviours are artefacts of captivity, since animals do not express stereotypies in nature. From the perspective of breeding

animals in captivity for reintroduction, it will be important to ascertain how the fitness of stereotyping individuals in captivity translates to the fitness of these animals in the wild. I recommend that this be tested, and while some authors argue that it would adversely affect release success (Kolter & Zander 1995; Vickery & Mason 2003), this remains to be validated.

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