MEALWORM DISPENSERS AS ENVIRONMENTAL ENRICHMENT FOR CAPTIVE RODRIGUES FRUIT BATS (PTEROPUS RODRICENSIS)

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Abstract

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This study is an assessment of the use of mealworm dispensers as environmental enrichment devices for Rodrigues fruit bats (Pteropus rodricensis). Captive animals frequently receive easily consumed food at set times and locations, which often minimizes the time they spend searching for and processing food. The mealworm dispensers used in this study provide an unpredictable food source, which allows the link between foraging and feeding to be reinstated. Mealworm dispensers were placed into the Rodrigues fruit bat enclosure at the Jersey Wildlife Preservation Trust and the behaviour of the bats recorded over 14 days. For 7 days the dispensers were empty but, for the remaining 7, 20 mealworms were placed in each dispenser. The number of bats feeding declined with increasing time from initial food presentation in all cases, but the presence of mealworms in the dispensers decreased the rate of decline. In addition, the number of bats active within 20cm of the food in the dishes and on the heater tops increased significantly when mealworms were present. Although the presence of mealworms had no effect on the number of flights made by the group of bats as a whole, both the number of bats on the enclosure floor and the amount of aggression observed in the enclosure decreased when mealworms were present.

Installation of mealworm dispensers meant that the bats found food items as a consequence of their natural exploratory and foraging behaviour, and as such they provided important ingredients for approximating a natural habitat and improving welfare.

Keywords: animal welfare, environmental enrichment, foraging, fruit bats, Pteropus rodricensis

Introduction

Megachiroptera or old world fruit bats have, until recently, been generally accepted to be exclusively frugivorous. How these bats obtain sufficient quantities of protein has long been debated (Courts 1998), and it has been suggested that fruit bats may increase their protein intake by supplementing their diet with insects (Thomas 1982). However, until recently only two species of fruit bats had actually been observed eating insects (Roberts & Seabrook 1989; Parry-Jones & Augee 1991), although insect remains had been found in the intestines of other bats (Lim 1973; Start & Marshall 1976). Work at the Jersey Wildlife Preservation Trust (JWPT) provided further evidence for the ingestion of insects by these predominantly frugivorous animals. Courts (1997) described how two species of fruit bat at the JWPT

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(Livingstone's fruit bat [*Pteropus livingstonii*] and Rodrigues fruit bat [*Pteropus rodricensis*]) ate flying insects, which they trapped with their wings. Following this work, several fruit bat species were presented with dishes of live mealworms (*Tenebrio molitor*) and waxmoth larvae (*Galleria mellonella*). For the Rodrigues, the response was described as a 'feeding frenzy' (Courts personal communication 1998). This response to insect larvae has been explored as a possible means of environmental enrichment for the Rodrigues fruit bats. Pope (1997) offered dishes of mealworms to the bats, which investigated the dishes within 15min of presentation and proceeded to consume approximately 80 per cent of the mealworms. Although this provided the bats with a novel enrichment device, the enrichment only lasted as long as the mealworms and did not reinstate the natural link between foraging and finding food.

In their natural habitat, most animals spend a high proportion of their daily activity budget searching for, processing and eating food (Herbers 1981; Holst 1997). This behaviour is not necessarily driven by hunger, as animals have been shown to search for food rather than eat freely available identical food (Jensen 1963; Neuringer 1969, 1970; Carder & Berkowitz 1970; Singh 1970; Duncan & Hughes 1972; Inglis & Ferguson 1985), and certain animals have also been shown to prefer to 'work' for their food (Havelka 1956). Animals in captivity frequently receive food at set times and locations, often in an easily consumable form, and so the opportunity to forage is reduced to a minimum (Holst 1997).

The mealworm dispensers used in this study dispensed the mealworms in an unpredictable manner and, by encouraging the bats to look for the food, approximated the contingent nature of food in the wild. This unpredictability, combined with the obvious challenges associated with handling live food items, should have increased the complexity of the environment and increased the levels of social and physical stimulation. This has already been successfully implemented for a number of mammalian species; for example Shepherdson *et al* (1990) found that providing kinkajou (*Potos flavus*) with food that required exploratory and manipulative behaviour greatly increased rates of locomotion, exploration and foraging, which corresponded to reductions in the levels of stereotyped behaviour. The aim of this project was to assess the effect of mealworm dispensers on the activity of a colony of Rodrigues fruit bats.

Methods

Study species

This study focused on the Rodrigues fruit bat, a medium-sized member of the family Pteropodidae. Its body mass is typically 240–270 g and it has a forearm length of 120–140 mm, with adult males tending to be slightly larger than females (Kunz *et al* 1994). The species is endemic to Rodrigues Island (19°S, 63°E), 650km east of Mauritius Island in the western Indian Ocean (Carroll 1981; West & Redshaw 1987). An expedition to Rodrigues Island in 1974 highlighted the bat's critical rarity (Cheke & Dahl 1981) and in 1976 a captive-breeding programme was established by the JWPT. This, coupled with a gradual increase in wild numbers, has meant that the situation has improved. However, in 1990 the Rodrigues fruit bat was made an Appendix II species by the Convention on International Trade of Endangered Species, and in 1996 was listed as critically endangered in the IUCN Red List of Threatened Animals.

The group of Rodrigues fruit bats at the JWPT consisted of 79 individuals, of which 54 were adult males, 19 adult females and 6 unsexed juveniles. All the bats, (bar one adult male remaining from the 1976 capture expedition) were captive-born. The activity pattern of the

bats was similar to that of other *Pteropus* species in the wild (Walker 1964), as they exhibited two main activity peaks, one just before dusk and one just after dawn. Peak feeding times corresponded with the times the bats were most active (see Carroll [1979] for a detailed description of the behavioural repertoire of the Rodrigues fruit bat).

Husbandry

The bats were housed in a granite building consisting of a single light-tight room with public viewing area. The area available to the bats was approximately 7x5x4 m lxwxh with one of the original roof beams running horizontally about 2.5m from the floor and 2m from the rear wall. Several branches were suspended throughout the enclosure to provide feeding and roosting sites, and there were electric heaters on the back wall and the two sides of the enclosure. The heaters were about 0.5m from the floor and maintained a night-time temperature of 21°C and a daytime one of 26-28°C within the enclosure. The heaters were covered in mesh to prevent damage to the bats. In addition to this meshed area, there were five small mesh panels positioned on the walls. A strip of guttering was attached to each of these five mesh panels and to the three meshed heaters. The length of the guttering varied according to the mesh panel size, with the length falling roughly into two size categories: 'short' (0.5m) and 'long' (2m). There were two long strips of guttering, one on the back wall heater and one on the heater to the left of the public viewing area. The remaining six strips of guttering were all short and arranged around the enclosure as illustrated in Figure 1. The height of the guttering varied between the panels so that the guttering on the heaters was approximately 1m above the ground and the guttering on the five panels was 1.5-2 m from the ground.



Figure 1 Layout of the Rodrigues fruit bat enclosure at the JWPT. The public viewing area is at the top and there is a door at the bottom right leading to the keeper's kitchen. Open rectangles represent heaters and black circles are food dishes. The dispensers are represented by black boxes, and the guttering by thick black lines. Open circles and semicircles show the positions of water dishes.

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At feeding times, any uneaten food from the previous day was collected by the keepers and fresh food was placed into the eight strips of guttering, seven feeding dishes resting on the fixed perches around the enclosure and onto the top of the three heaters. There were six small water cups around the enclosure and water was supplied *ad libitum*. The bats were fed twice a day, once at 1000h and then at 1600h. The morning feed consisted of 8kg of mixed fruit, and the afternoon feed was 0.7kg of Leaf-Eater Primate Diet (Special Diet Services, Witham, UK). In addition to the feed, a selection of forage was occasionally scattered around the enclosure when the afternoon feed was taken in. The exact composition and quantity of forage varied greatly depending on availability.

Lighting was supplied by three sets of lights which provided light at varying intensities to simulate daytime, twilight and night-time. The lights were covered in mesh to protect the bats from heat damage. Although the bats were kept on a reverse light:dark schedule to allow zoo visitors to view active bats, the photoperiod was similar to the seasonal variation of Rodrigues Island. At the time of the study, the lights went off at 1015h and came on at 2215h.

Enrichment Programme

The experiment was conducted over a period of 20 days between 21 July and 9 August 1998. On day 1, the eight empty mealworm dispensers were placed into the enclosure over each of the strips of guttering. The dispensers consisted of plastic boxes (12.5x15x10 cm) with three 6mm diameter holes in the base, through which the mealworms could wriggle (Figure 2). The dispensers had opaque lids that prevented the bats from removing the mealworms from above and were attached to the mesh panels around the enclosure so that they were approximately 10cm above the guttering. This meant that, during the enrichment programme, when mealworms were placed into the dispensers they would fall through the holes in the base of the dispensers and into the guttering where the bats could find them. As the dispensers were only above the guttering, the bats would find mealworms solely in the guttering, and only when mealworms had been placed in the dispensers. In addition, the bats received mealworms in their morning and afternoon food dishes on days 1 to 4. As the



Figure 2 Illustration of a mealworm dispenser. Each dispenser was 12.5x15x10 cm, with three 6mm diameter holes in the base and an opaque lid. Wire was threaded through the slots in the sides of the dispenser in order to attach it to the enclosure wall.

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bats had not previously received mealworms, this procedure was designed to encourage the bats to view the mealworms as a food item. Each morning at about 0800h the bat enclosure was cleaned and any uneaten food removed: during this period the dispensers were removed and also cleaned.

Observations

Data collection began on day 5. Following the morning feed, the bats were observed for 1h. Observations were made using a combination of instantaneous and behaviour sampling of the whole group (Martin & Bateson 1993). Although focal animal sampling would have had the advantage of identifying exactly how the mealworm dispensers influence individuals' time budgets, it was impossible to accurately identify individual bats. The 1h period following feeding was split into six 10min periods. At the start of each period, the number of bats feeding at the 10 food platforms without dispensing boxes (ie the seven feeding dishes and three heater tops) was recorded, along with the number of bats feeding at the lengths of guttering, all of which had dispensers attached above them. In addition, the number of active bats (ie not roosting) within 20cm of the feeding platforms was recorded for platforms with and without dispensers. Previous studies have shown that these fruit bats may land and crawl on the floor to recover fallen food items (Carroll 1979) and, in order to gain an insight into the prevalence of this behaviour, the number of bats on the floor of the enclosure was also recorded at the start of each 10min period. Recording all the data for each 10min period took approximately 70s. During minutes 5–9 of each 10min period, the number of flights made by the group of bats as a whole, regardless of length, and the number of escalated fights were noted. Escalated fights typically involved a pair of bats stabbing at each other with their hooked thumbs, making frantic movements towards each other and loud vocalizations. Fights that did not involve all of these behaviours were not included. A further two 1h observation sessions were carried out 2 and 4h after the morning feed, using exactly the same recording technique as used in the first hour. All of the observations were made from the public viewing area as previous studies have shown that the presence of a single observer, or even many members of the public, did not influence the behaviour of these bats (Carroll 1979).

Data were collected for 7 days when there were no mealworms in the dispensers. On days 13–20, 20 mealworms were placed into each dispenser after it had been cleaned, but before it was replaced in the enclosure (making a total of 160 mealworms available in the feeders). Observational data were collected using exactly the same method as for the previous behavioural data collection period and, in addition, the number of mealworms remaining in the dispensers and guttering was recorded for each of the 7 days.

Statistical analysis

Data were analysed using the statistical package SPSS (Norusis 1998), and statistical significance was considered at the P < 0.05 level. When there was a linear relationship between the variable being recorded and the time from the morning feed, the influence of the presence of mealworms in the dispensers was assessed by comparing the slope and elevation of the lines for the two categories (ie with mealworms in the dispensers and without mealworms in the dispensers). However, where no clear relationship existed between the time from the morning feed and the variable being recorded, the data from each hour of observations were grouped and the influence of the presence or absence of mealworms in the dispensers on the 3h of observation analysed. All probabilities quoted in the paper are for two-tailed statistical tests.

Results

Although the bats appeared to treat the mealworms with a great deal of caution on day 1, by day 4 presentation of food dishes containing mealworms resulted in a flurry of activity as the bats approached the food dishes and found the mealworms. The bats responded very enthusiastically to the mealworms, preferentially selecting them over other food items. When the bats found a mealworm, they would masticate it before swallowing it and resuming the search for another mealworm. This excitement was similar to the 'feeding frenzy' seen by Courts (personal communication 1998). For the most part, when the dispensers were empty the bats remained completely oblivious to their presence. However, when there were mealworms in the dispensers the bats frequently hung from their outer edge to examine the guttering immediately below.

On days 13–20, between 97 and 100 per cent of the mealworms placed in the dispensers successfully fell out. Of these mealworms, only eight were recovered from the guttering during the morning clean over the whole week. Pilot studies using the dispensers showed that 85 per cent of the mealworms fell out of the dispensers in the first 4h (O'Connor unpublished data).

The bats consumed the vast majority of the food placed into their enclosure and there was no change in the amount of fruit and Leaf-Eater Primate Diet consumed by the bats during the course of the experiment (JWPT staff personal communication 1998).



Figure 3 Number of bats (mean \pm SEM) feeding at the guttering. Open circles and the dotted line represent data collected when the mealworm dispensers were empty. Closed circles and the solid line represent data collected when there were mealworms in the dispensers. See text for statistical analysis.

Effect of mealworm dispensers on the number of bats feeding and the number near feeding platforms

When the number of bats feeding at the guttering with the mealworm dispensers was plotted against time from the morning feed, both sets of data (ie without mealworms [NM] and with mealworms [M]) showed a decrease with increasing time from the feed (linear regression, NM: adj. $r^2 = 0.33$, n = 147, P < 0.001; M: adj. $r^2 = 0.10$, n = 147, P < 0.001). The slopes of these two regressions differed significantly (*t*-test, $t_{38} = 2.02$, P < 0.05), with the presence of mealworms in the dispensers resulting in a slower decrease in the number of bats feeding at the guttering (Figure 3).

Likewise, the number of bats feeding at the food dishes and heater tops tended to decrease with increasing time from the morning feed (linear regression, NM: adj. $r^2 = 0.55$, n = 147, P < 0.001; M: adj. $r^2 = 0.24$, n = 147, P < 0.001), with the presence of mealworms decreasing the rate of decline of number of bats feeding at these sites (*t*-test, $t_{38} = 3.18$, P < 0.01; Figure 4). This was despite the fact that, even when they were present in the dispensers, mealworms fell into the guttering and not into the food dishes or onto the heater tops.



Figure 4 Number of bats (mean ± SEM) feeding at the seven food dishes and three heater tops. Symbols as in Figure 3. See text for statistical analysis.

The number of bats within 20cm of the feeding dishes and heater tops decreased with time from the morning feed (linear regression, NM: adj. $r^2 = 0.22$, n = 147, P < 0.001; M: adj. $r^2 = 0.11$, n = 147, P < 0.001) and although the slopes of these lines were not significantly different, they did differ in elevation (*t*-test, $t_{291} = 2.33$, P < 0.01; Figure 5) with the presence of mealworms in the dispensers increasing the number of bats near these feeding platforms. This was despite the fact that mealworms never fell into the dishes or onto the heater tops.









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There was no linear relationship between the number of bats within 20cm of the guttering and the time from the morning feed for either the period when mealworms were present in the dispensers or when they were absent. In order to analyse differences between the 3h of observations, the data for each hour were grouped. Analysis revealed that the presence of mealworms in the dispensers did not affect the number of bats within 20cm of the guttering (*t*-test, $t_2 = 1.08$, ns; Figure 6).

Effect of mealworm dispensers on fights, flights and floor use

When there were no mealworms in the dispensers, the number of escalated fights within the enclosure decreased with time from the morning feed (linear regression, adj. $r^2 = 0.22$, n = 147, P < 0.001). The slope of the regression line representing the decline in fights with increasing time from the morning feed was significantly different from zero (*t*-test, $t_{146} = 7.33$, P < 0.001). When mealworms were placed in the dispensers, the number of escalated fights was consistently very low. The slope of the line representing the relationship between the number of fights and time from the morning feed was not significantly different from zero (*t*-test, respectively).



Figure 7 Number of fights (mean ± SEM) in the enclosure. Symbols as in Figure 3. See text for statistical analysis.

As there was no linear relationship between either the number of flights within the enclosure or the number of bats on the floor and the time from the morning feed, the data for each hour of observation were grouped to enable further analysis. Although the presence of mealworms in the dispensers had no effect on the number of flights made by the bats (*t*-test, $t_2 = 0.41$, ns; Figure 8), the number of bats on the enclosure floor was consistently lower when mealworms were placed in the dispensers than when they were empty (*t*-test, $t_2 = 29.29$, P = 0.001; Figure 9).



Figure 8Number of flights (mean ± SEM) in the enclosure. Symbols as in Figure6. See text for statistical analysis.



Figure 9 Number of bats on the floor (mean ± SEM) in the enclosure. Symbols as in Figure 6. See text for statistical analysis.

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Discussion

The unpredictable pattern with which the mealworms emerged from the dispensers minimized the certainty of availability while maximizing the functional consequences of foraging behaviour, which has been shown to be an effective enrichment technique (Shepherdson et al 1993). The most notable effect of the presence of mealworms in the dispensers was that it slowed the decrease in the number of bats feeding both at the guttering below the dispensers and at the feeding dishes and heater tops. The increased number of bats feeding at the food sites could mean one of two things: either each bat was spending longer at the food or there was an overall increase in the number of bats visiting the food during the observation time. As the number of flights made by the colony was lower when mealworms were present in the dispensers, it seems likely that the elevated number of bats at the food stations was due to the bats being more sedentary and spending longer at the food. As previous studies have shown that Rodrigues fruit bats rarely actually eat at the food dishes, preferring to carry their food to a perch (Carroll 1979), an increase in the time an individual bat spent at the feeding area meant that it probably spent more time foraging (ie actively looking for a food item). However, individual identification and continuous observation of the bats would be needed to identify the exact cause of the increase in numbers at the food stations.

Perhaps the most interesting effect of the presence of mealworms in the dispensers was that it increased the number of bats at the food dishes and heater tops, despite the fact the bats would not find mealworms at those locations. While it is obvious that the presence of mealworms in the dispensers would make the guttering more attractive, it is harder to understand why the bats should also spend more time at the other dishes and heater tops. One possibility is that, having noticed the mealworms in the guttering, the bats associated mealworms with the normal food and so looked for them in the dishes and on the heater tops. This was an unexpected benefit, as it meant that it was not necessary for dispensers to be present at all of the dishes to make all the food seem more interesting and thus increase foraging.

The differing results for the number of bats within 20cm of the food dishes and guttering could be misleading: if the mealworms did make the food more stimulating, it would be easier for bats to gain access to the guttering, as it was larger, than to the relatively small dishes. Even the inclusion of the data for the heater tops in the group 'food dishes and heater tops' would not disguise the queuing effect resulting from the small dishes limiting access. Thus, we saw an increase in the number of bats within 20cm of the food dishes and heater tops when mealworms were in the dispensers but no effect on the number of bats within 20cm of the guttering.

The fact that the presence of mealworms in the dispensers had no effect on the number of flights within the enclosure offers support for the hypothesis that the increase in number of bats at the food is a result of longer visits and not a consequence of more bats visiting the food. The consistency of flight frequency over the observation period is in agreement with a study carried out on the colony in 1979 (Carroll 1979). However, the absolute number of flights was lower than previously found. It is possible that this was a result of the smaller colony size in 1979 (23 bats as opposed to 79), and the lower number of obstacles (the enclosure contained fewer branches) which meant that flight was more risky for the bats in 1998 (ie the bats were more likely to bump into other bats or branches). In addition, flights would have been easier for the observer to see in 1979.

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The number of escalated fights when there were no mealworms in the dispensers decreased with time from the morning feed. It could be suggested that as the number of bats at the feeding dishes decreased, so the probability of two bats fighting over space and individual food items decreased. Once the bats had eaten sufficient food, and moved away from the dishes, the level of aggression in the enclosure should have decreased. A well-defined territoriality has been observed in this colony of bats (Russo 1994) and it could be that the initial presence of food within the enclosure, and the movement of the bats towards the food, meant that territories were invaded. As the abundance of food decreased, so did the movement of the bats and subsequently territorial boundaries were observed. Alternatively, it has been suggested (Carroll 1978) that the routine cleaning of the enclosure may agitate the bats and perhaps the aggression observed in the first hour following the cleaning and feeding was a consequence of a person in their enclosure during this time.

When mealworms were present in the dispensers, the amount of aggression in the enclosure decreased markedly. This increase in foraging and reduction in aggression has also been seen in other enrichment studies, for example stump-tailed macaques (*Macaca arctoides*) provided with litter in which they could forage for grain increased their level of foraging by a factor of five while reducing aggression (Anderson & Chamove 1984). One hypothesis for this decrease is that the bats become so preoccupied with the food that they fail to react to the invasion of their territories and that, once at the food, the items immediately closest to them are so interesting that they do not react to the close proximity of other bats. Alternatively, more bats may be feeding at the food and hence fewer territory owners were in their territories to defend them.

Unlike their usual food, the mealworms were live and so required a certain degree of skill and ingenuity. As the bats' attention was focused on the mealworms, they may have been less conscious of the movement of other bats. The spacing and unpredictable pattern of emergence of the mealworms from the dispensers was such that, although they were a highly favoured food item, it was impossible for dominant bats to efficiently monopolize access to them. This meant that aggression levels would not be elevated due to fights over access to the mealworms. On days 1–4, the feeding frenzy observed was probably a result of the bats being presented with a food dish containing fruit and a relatively large quantity of readily available mealworms. However, on days 13–20 the mealworms were presented in an unpredictable temporally spaced manner which meant that there was unlikely to be the feeding frenzy that may have led to increased levels of aggression as bats fought over mealworms. In order to analyse why the amount of aggression decreased, a more extensive study is needed in which individuals could be identified and their interactions with other bats recorded.

The change with time in the number of bats using the floor from the morning feed showed a similar pattern for both conditions (ie mealworms and no mealworms), with the number of bats on the floor being highest during the second hour of observations. Captive Rodrigues fruit bats sometimes descend to the floor to search for fallen food (Carroll 1979). One hypothesis for the increase in numbers on the floor during the second hour is that the decrease in the amount of food in the dishes, combined with the increase in the amount of food on the floor. Food stealing is often seen in Rodrigues fruit bats (Carroll 1979) and it is not unusual for a struggle to develop during which the food falls to the floor, thus the high level of aggression in the first hour would have led to a large amount of food being present

on the floor during the second hour of observations. By the third hour of observations, the amount of food available would have decreased, any food dropped in the first hour would have been recovered and the reduced aggression in the second hour would have meant that there was little new food on the floor.

The lower numbers of bats on the floor when mealworms were in the dispensers could be as a result of the decrease in aggression. Floor feeding was probably performed predominantly by low ranking bats which did not possess a territory (Russo 1994). When mealworms were present in the dispensers there was an overall decrease in aggression which may have meant that low ranking bats gained access to food that they would normally have been excluded from. Therefore, there was less need to feed on the floor.

The roles of modern zoos are conservation, education, recreation and research (Tudge 1992). In order to educate the public, we need not only to provide animals for them to see, but also to provide animals which are behaving in a natural manner (Sommer 1972; Coe 1985; Maple & Finlay 1987; Catlow *et al* 1997). In addition, natural behaviour is a prerequisite to worthwhile research on the animals (Catlow *et al* 1997). Bats are frequently victims of 'bad press' as they take a starring role in so many popular horror stories. Presenting bats to the public in a way that portrays them as aggressive propagates this myth. Simple enrichment devices, such as the dispensers used in this study, decrease aggression and provide the opportunity for the public to see the bats behaving in a more naturalistic manner (eg foraging).

Animal welfare implications

Installing these mealworm dispensers meant that the fruit bats were in an environment where they could find food (mealworms) as a consequence of their natural exploration and foraging behaviour, and this approximated to a natural habitat and improved welfare (Shepherdson *et al* 1993). Aside from the advantages they bring in encouraging the expression of a more realistic behavioural repertoire and time budget, the feeders are inexpensive and easy to maintain. As has been shown in the past (Law *et al* 1990; Herron 1997) it is often the simplest ideas that are the most effective in providing environmental enrichment, as these ideas are more likely to be used. Although this study has focused on Rodrigues fruit bats, the dispensers could be used with other captive bats, and indeed could be used for other animals if the mealworms could be replaced with relevant insect food.

It should be noted that, as with other enrichment devices (Ings *et al* 1997), the novelty value of the dispensers may decrease with time, and further study would be necessary to assess the long-term effects of the use of mealworm dispensers. Although this study suggests that the use of mealworm dispensers would undoubtedly benefit the animals in the short term, they are not a complete solution to the environmental enrichment arms race that must exist between keepers and captive animals.

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References

- Anderson J R and Chamove A S 1984 Allowing captive primates to forage. In: *Standards in Laboratory* Animal Management (part 2). Universities Federation for Animal Welfare: South Mimms, UK
- Carder B and Berkowitz K 1970 Rats' preference for earned in comparison with free food. Science 167: 1273-1274
- **Carroll J B** 1978 Behavioural observations on the Rodrigues fruit bat *Pteropus rodricensis* following a move to a new accommodation and reversal of the light/dark regime. *Dodo, Journal of the Jersey Wildlife Preservation Trust* 15: 52-60
- **Carroll J B** 1979 The general behavioural repertoire of the Rodrigues fruit bats *Pteropus rodricensis* in captivity at the Jersey Wildlife Preservation Trust. *Dodo, Journal of the Jersey Wildlife Preservation Trust 16*: 51-59
- Carroll J B 1981 The wild status and behaviour of Rodrigues fruit bats *Pteropus rodricensis*. A short report of the 1981 field study. *Dodo, Journal of the Jersey Wildlife Preservation Trust 18:* 20-29
- Catlow G, Ryan P M and Young R J 1997 Please don't touch we're being enriched! In: Proceedings of the 3rd International Conference on Environmental Enrichment pp 209-217. 12-17 October 1997 Orlando, USA
- Cheke A S and Dahl J F 1981 The status of bats on western Indian Ocean islands, with special reference to *Pteropus. Mammalia* 45: 205-238
- Coe J C 1985 Design and perception: making the zoo experience real. Zoo Biology 4: 197-208
- **Courts S E** 1997 Insectivory in captive Livingstone's and Rodrigues fruit bats *Pteropus livingstonii* and *P. rodricensis* (Chiroptera: Pteropodidae): a behavioural adaptation for obtaining protein. *Journal of Zoology, London 242:* 404-410
- **Courts S E** 1998 Insectivorous habits of fruit bats. In: *Pteropus, The Lubee Foundation Technical Bulletin* 4 4 pp. The Lubee Foundation Inc: Gainesville, USA
- Duncan I J H and Hughes B O 1972 Free and operand feeding in domestic fowls. Animal Behaviour 20: 775-777
- Havelka J 1956 Problem seeking behavior in rats. Canadian Journal of Psychology 10: 91-97
- Herbers J M 1981 Time resources and laziness in animals. Oecologia 49: 252-262
- **Herron S** 1997 Environmental enrichment devices currently in use at Jersey Wildlife Preservation Trust. In: *Proceedings of the 3rd International Conference on Environmental Enrichment* pp 300-312. 12-17 October 1997 Orlando, USA
- Holst B 1997 The ethics of environmental enrichment. In: Proceedings of the 3rd International Conference on Environmental Enrichment pp 45-48. 12–17 October 1997 Orlando, USA
- Inglis I R and Ferguson N J K 1985 Starlings search for food rather than eat freely available identical food. Animal Behaviour 34: 614-617
- Ings R, Waran N K and Young R J 1997 Effect of wood-pile feeders on the behaviour of captive bush dogs (Speothos venaticus). Animal Welfare 6: 145-152
- Jensen E D 1963 Preference for bar pressing over 'free loading' as a function of number of rewarded presses. Journal of Experimental Psychology 65: 451-454
- Kunz T H, Allgaier A L, Seyjagat J and Caligiuri R 1994 Allomaternal care: helper-assisted birth in the Rodrigues fruit bat, *Pteropus rodricensis* (Chiroptera: Pteropodidae). *Journal of Zoology, London 232:* 691-700
- Law G, Boyle H, Johnston J and MacDonald A 1990 Food presentation, part 2: cats. Ratel 17: 103-106
- Lim B L 1973 Breeding patterns, food habits and parasitic infestation in Gunong Brinchang. Malayan Nature Journal 26: 6-13
- Maple T L and Finlay T W 1987 Postoccupancy evaluation in the zoo. Applied Animal Behaviour Science 18: 5-18
- Martin P and Bateson P P P G 1993 Measuring Behaviour. An Introductory Guide. Cambridge University Press: Cambridge, UK

Neuringer A J 1969 Animals respond for food in the presence of free food. Science 166: 399-401

Animal Welfare 2000, 9: 123-137

Neuringer A J 1970 Many responses for food reward with free food present. Science 169: 503-504

Norusis M J 1998 SPSS 8.0 Guide to Data Analysis. Prentice Hall: New Jersey, USA

- Parry-Jones K and Augee M L 1991 The diet of flying foxes in the Sydney and Gosgord areas of New South Wales, based on sighting reports 1986–1990. Australian Zoologist 27: 49-54
- Pope B 1997 Insectivory as an enrichment option with the Rodrigues fruit bats (*Pteropus rodricensis*). In: *Proceedings of the 3rd International Conference on Environmental Enrichment* pp 383-385. 12–17 October 1997 Orlando, USA
- Roberts P and Seabrook W A 1989 A relationship between black rats (*Rattus rattus*), Seychelles fruit bats (*Pteropus seychellensis aldabrensis*) and the coccoid (*Icerya seychellarum*) (Insecta, Homoptera) on Aldabra Atoll, Seychelles. Journal of Zoology, London 218: 332-334
- Russo D 1994 Feeding Activity and Behaviours Displayed at the Stations in a Colony of Rodrigues Fruit Bats Pteropus rodricensis. Unpublished report of the JWPT Summer School Projects pp 95-116
- Shepherdson D, Brownback T and Tinkler D 1990 Putting the wild back into zoos: enriching the zoo environment. Applied Animal Behaviour Science 28: 300
- Shepherdson D, Carlstead K, Mellen J D and Seidensticker J 1993 The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology* 12: 203-216
- Singh D 1970 Preference for bar pressing to obtain rewards over freeloading in rats and children. Journal of Comparative Psychology 73: 320-327

Sommer R 1972 What do we learn at the zoo? Natural History 81: 25-26, 81-84

- Start A N and Marshall A G 1976 Nectivorous bats as pollinators of trees in West Malaysia. In: Burley J and Stiles B T (eds) Variation, Breeding and Conservation of Tropical Forest Trees. Academic Press: London, UK
- **Thomas D W** 1982 The Ecology of an African Savannah Fruit Bat Community Resource Partitioning and Role in Seed Dispersal. Unpublished PhD thesis, University of Aberdeen, UK
- **Tudge C** 1992 Last Animals at the Zoo: How Mass Extinction can be Stopped. Oxford University Press: Oxford, UK
- Walker E P 1964 Mammals of the World, Volume 1. The John Hopkins Press: Baltimore, USA
- West C C and Redshaw M E 1987 Maternal behaviour in the Rodrigues fruit bat Pteropus rodricensis. Dodo, Journal of the Jersey Wildlife Preservation Trust 24: 68-81