The impact of exhibit type on behaviour of caged and free-ranging tamarins

Kayley Bryan[a], Samantha Bremner-Harrison[a], Eluned Price[b] and Dominic Wormell[b]

[a] School of Animal, Rural and Environmental Sciences, Nottingham Trent University, Brackenhurst Lane, Southwell, Nottinghamshire. NG25 0QF.

[b] Durrell Wildlife Conservation Trust, Les Augrès Manor, Trinity, Jersey, Channel Islands, JE3 5BP, United Kingdom.

Corresponding Author:

Kayley Bryan

50 Howden Road,

Leicester.

LE2 9AU.

Phone: 07926867442

Email: Kayley_Bryan@hotmail.co.uk

Highlights

- Captive environments often lack required stimuli to preserve natural behaviour
- This study compared behaviour of free-ranging and caged tamarins
- Significant differences in mean rates of behaviour found between conditions
- Free-ranging tamarins exhibited increased locomotion and proficient environment use
- Free-ranging exhibit conducive to the exhibition of natural behaviours

Abstract

The lack of appropriate stimuli associated with captive environments has been documented to cause several behavioural and physiological issues in captive species, including loss of natural behaviours, psychopathologies and decreased reproductive success. Providing free-ranging, naturalistic exhibits that replicate elements of a species' natural environment is advocated as a means of promoting and preserving the natural behavioural repertoire in captive species. Exhibition of natural behaviour is considered beneficial to conservation in terms of increased animal welfare, reintroduction success, education and research. This study assessed differences in behaviour of emperor and pied tamarins housed in free-ranging and caged exhibits at Durrell Wildlife Park, to determine the impact of exhibit type. Free-ranging tamarins were expected to exhibit a repertoire of behaviours more similar to that of wild tamarins, based on their access to a more natural and complex environment. Data was collected on a variety of behaviours, including activity, substrate use and communication, using instantaneous and one-zero sampling at 30 second intervals. Findings indicated that both free-ranging and caged tamarins exhibited natural behaviours; however, there were significant differences in mean rates of behaviours between conditions. Free-ranging tamarins exhibited significantly higher rates of locomotion (emperors: $P < 0.001$; pieds: $P < 0.001$), long calls (pieds: $P < 0.05$) and alarm calls (emperors: $P < 0.05$), and displayed competent use of the environment in terms of natural substrate use (emperors: $P < 0.001$; pieds: $P < 0.01$) and appropriate interspecific interactions. Caged tamarins exhibited significantly higher rates of affiliative (emperors: $P < 0.001$; pieds: $P < 0.05$) and agonistic (emperors: $P < 0.005$) intraspecific interactions and time spent in contact (emperors: $P < 0.05$; pieds:

$P < 0.05$), which was largely attributed to spatial restrictions imposed by caged exhibits. This study, consistent with existing literature, indicated that the free-ranging exhibit was conducive to the expression of a behavioural repertoire more similar to that of wild tamarins. This was probably a result of the increased behavioural opportunities available in the free-ranging exhibit, highlighting their importance in promoting wild-type behaviours. However, some mean rates of behaviour were still noticeably less than those documented in wild counterparts. Methods to further promote natural behaviours in both exhibits are recommended to facilitate *ex situ* and *in situ* conservation efforts.
Keywords: Captivity, emperor tamarin, free-ranging, natural behaviour, naturalistic exhibit, pied tamarin

1.0 Introduction

In captivity, animals are faced with an environment that differs substantially from their natural habitat and is often lacking in appropriate stimuli (McPhee and Carlstead, 2010). Less time is required for natural activities such as foraging, mate-seeking and predator avoidance, and thus, these behaviours often decrease (Shepherdson, 1994; Prescott and Buchanan-Smith, 2004) and time spent on other activities, including abnormal behaviours, may increase (Jaman and Huffman, 2008; McPhee and Carlstead, 2010). Additionally, natural and artificial selection pressures within the captive environment can alter behaviours and traits to those that confer greater survivorship in captivity, resulting in genetic, morphological and phenotypic divergence from wild counterparts (Shepherdson, 1994; Williams and Hoffman, 2009). The inability to express natural behaviour in captivity can have severe implications for conservation in terms of decreased animal welfare, reintroduction success and species recovery (McPhee and Carlstead, 2010).

As a result, modern zoos increasingly endeavour to provide complex, naturalistic exhibits (Davey, 2006; Fabregas *et al.*, 2012), on the assumption that the closer a captive environment resembles a species' natural environment, the more likely it is to provide opportunities to meet their biological and behavioural needs and elicit a full range of natural behaviour patterns (Maple and Finlay, 1989; Chang *et al.*, 1999; Morgan and Tromborg, 2007; Hosey *et al.*, 2009). Indeed, wild-type activity budgets have been documented across numerous species housed in naturalistic exhibits, including mandrills (Chang *et al.*, 1999); Hanuman langurs (Little and Sommer, 2002), Indian leopards (Mallapur *et al.*, 2002) and Sulawesi macaques (Melfi and Feistner, 2002). Exhibition of natural behaviour is generally considered to be an indicator of good welfare and crucial to reintroduction success (Melfi and Feistner, 2002; Melfi *et al.*, 2004; McPhee and Carlstead, 2010).

Free-ranging zoo exhibits allow animals to move more or less freely within a naturalistic environment (Price *et al.*, 2012). Individuals are afforded a degree of control in their environment, allowing them to be behaviourally flexible and exhibit adaptive responses to novel situations, as required *in situ* (Shepherdson, 1994; Chang *et al.*, 1999). Studies of free-ranging callitrichids in comparison to caged individuals have reported adaptive behaviour and increased natural behaviours, including vigilance, feeding, locomotion and wider substrate use (Price *et al.*, 1989, 1991, 2012; Price, 1992; Moore, 1997), reduced mortality and increased success in weaning offspring (Steinmetz *et al.*, 2011) and lower levels of injury, illness or fighting (Beck *et al.*, 2002).

However, it has been argued that even naturalistic exhibits can never fully replicate the pressures and unpredictability found *in situ* (Hosey, 2005; McPhee and Carlstead, 2010). Abnormal behaviours and behavioural deficits have still been documented in captive species housed in naturalistic exhibits, suggesting that a naturalistic appearance is not always synonymous with increased functionality and any associated benefits (Shepherdson *et al.*, 1998; Melfi *et al.*, 2004; McPhee and Carlstead, 2010). Furthermore, Hosey (2005) argues that a lack of certain wild-type behaviours does not necessarily signify reduced welfare, as not all natural behavioural opportunities can be replicated.

The relationship between free-ranging captive exhibits and reintroduction success is also ambiguous (Beck *et al.*, 2002; Price *et al.*, 2012). Some studies report increased survival as a result of exposure to such environments (Miller *et al.,* 1990; Biggins *et al.,* 1999; Valladares-Padua *et al.,* 2000), whilst others found no additional survival benefits (Beck *et al.,* 2002; Stoinski and Beck, 2004). However, the definition of "free-ranging" used in the latter studies is debatable (Price *et al.,* 2012). Therefore, increasing knowledge of the effect of free-ranging exhibits on behavioural repertoires would be beneficial, and would help to identify the best exhibit types for preserving and promoting natural behaviours. The majority of studies in this field have investigated the movement and/or adaptation of individuals to more naturalistic exhibits (e.g. Box and Rohrhuber, 1993, Chang *et al.,* 1999, Little and Sommer, 2002, Mallapur *et al.,* 2002; Armstrong and Santymire, 2013), with fewer studies concerned with free-ranging exhibits and choosing to focus on specific aspects of behaviour (Price *et al.,* 1989, Price, 1992; Stafford *et al.,* 1994; Burrell and Altman, 2006; Steinmetz *et al.,* 2011). This study investigated differences across a variety of behaviours in free-ranging and caged bearded emperor tamarins (*Saguinus imperator subgrisescens*) and pied tamarins (*Saguinus bicolor*), to determine the impact of exhibit type on behaviour. We expected that free-ranging tamarins of both species would exhibit a behavioural repertoire that more closely resembled that of their wild counterparts, based on their access to a more complex and naturalistic environment.

2.0 Methods

2.1. Subjects and housing

Subjects consisted of free-ranging emperor tamarins (FRE), free-ranging pied tamarins (FRP), caged emperor tamarins (CE) and caged pied tamarins (CP) (Table 1). All subjects were captive born and housed at Durrell Wildlife Park, Jersey, United Kingdom. Subjects were chosen based on similar social and age structures where possible, as well as comparable exhibit design within each condition. CE, CP and FRP were housed in male-female pairs. FRE consisted of mother, father, son and daughter. Groups had been established for varying amounts of time ranging from 3 months to 5 years. All subjects were parent-reared, except one hand-reared male CP.

Free-ranging tamarins (FRT) were housed in 'Tamarin Woods' which was partially accessible to the public. The FRE and FRP study groups were based in separate sheds approximately 50 m apart, but all FRT had constant access to a much larger area via vegetation and fencing and interacted frequently (see Price *et al.*, 2012 for further details). As such, the main area utilised on a daily basis by FRT (as denoted by keepers) was used when referring to the free-ranging exhibit in this study; see Figure 2.1. Golden-lion tamarins (*Leontopithecus rosalia*) were also present in the free-ranging exhibit but were not included in this study due to a lack of caged individuals for comparison.

Limited availability of individuals for this study resulted in selection of caged tamarins (CT) housed in slightly different exhibits (Table 2). The majority of CT were housed in off-show exhibits, but one pair of CE were housed in an on-show exhibit. All CT had 24-hour access to their sheds and outside areas whilst FRT were secured in their shed at night due to predation risks and declining temperatures. Indoor shed areas were furnished similarly across species and conditions; each unit consisted of ropes, wooden platforms, nestboxes and water bottles. Floors were covered with wood shavings and a temperature of 23◦C-27◦C was maintained via thermostats using 80W heat lamps (see Wormell and Brayshaw, 2000, for full details). Husbandry routines were also comparable across species and conditions. All tamarins were fed a diet of primate pellets, mixed fruit and vegetables, and insects (see Wormell, 2010), with food given three times a day (08.30-09.00h, 11.30-12.30h and 15.00-16.00h), except for FRE. Due to difficulty with recall, FRE were fed a small training treat before release at 09.00h and were encouraged to return at around 10.30h for breakfast and 15.00h for dinner. FRP were released at around 09.00h, recalled at 12.00h for lunch and a visitor talk, and retired at around 16.00h.

2.2. Data collection

2.2.1 Pilot study and ethogram design

Ad libitum sampling was carried out for five days prior to data collection to facilitate ethogram design, determine sampling techniques and allow for identification of individuals. An ethogram (Table 3) was developed using data from the pilot study and similar studies. Behaviours included were considered to be representative of the behavioural repertoire of tamarins, including environment use. Categories for height above ground were created based on the maximum height of the caged exhibits (approximately 4 m). Social spacing categories were based on the maximum distance that CT could move apart while remaining simultaneously visible.

2.2.2 Behavioural data

Data collection occurred during 20 minute sessions, 12 times per day for 5 days a week, from 4th June 2014 to 23rd July 2014. To control for diurnal variation in behaviour, observations were divided into three time periods: 09.00-10.30h, 11.00-12.30h and 13.00-14.30h. Observations ceased for all tamarins at 14.30h to prevent bias due to restrictions imposed by husbandry routines for FRE. Data were collected on focal animals using instantaneous sampling at 30 second intervals combined with one-zero sampling (Martin and Bateson, 1993). Focal animals were selected in a predetermined order, so that each animal was observed for equal amounts of time within each time period, ensuring equal representation in the final sample. At each 30 second sample point, the location, activity, substrate type (diameter and orientation), height above ground (m) and social spacing (to the nearest metre) of the focal animal were recorded. One-zero sampling was used to record the occurrence of long calls, alarm calls, scent marking, locomotion type and social and sexual interactions within each 30 second interval. Locomotion, social and sexual behaviours were recorded using instantaneous and one-zero sampling to obtain data for activity budgets, as well as the occurrence of specific behaviours. Using a combination of instantaneous and one-zero sampling ensured that data was collected on a wide variety of behaviours.

Data were only collected when individuals were outdoors, due to poor visibility in sheds and the fact that exhibits mainly differed in terms of outdoor access. Otherwise, individuals were recorded as ‘in shed’ or ’not visible’. Sessions when individuals were entirely ‘not visible’ or had been restricted to their shed were repeated. Individuals which had a mean percentage of visibility more than one standard deviation from the mean visibility of all individuals within that condition were observed for an additional hour, increasing the amount of data for analysis.

2.2.3 Ethical considerations and risk assessment

This study received ethical clearance by The School of ARES Ethical Review Group at Nottingham Trent University prior to data collection.

2.3 Data analysis

As some individuals were not visible considerably more than others, instantaneous and one-zero scores were converted to mean rates per hour of time visible for all behaviours, except ‘not visible’. To determine if there were any significant differences in visibility, all visible and not visible data points were used.

For the purpose of analysis, the social behaviour category was condensed into ‘affiliative’ (play, allogrooming and affection) and ‘agonistic’ (aggressive and submissive) interactions. The social spacing category was condensed into ‘contact’ (<1m) ‘proximity’ (1-4m) and ‘distant’ (>4m). The sexual interactions category was condensed into one overall category. Any behavioural categories with no values for both free-ranging and caged conditions were excluded from statistical analysis.

Therefore, 'other', and 'ground' were excluded for emperors. As CT could not reach heights of '>5m' this category was excluded from statistical analysis. The younger animals in the FRE group did not exhibit sexual behaviour, thus, this category was also excluded from analysis for emperors.

Statistical analyses were carried out using IBM SPSS statistics version 21. Mann-Whitney *U* tests were used to assess differences in behaviour between FRT and CT for each species (e.g. Box and Rohrhuber, 1993, Mallapur *et al.*, 2002, Steinmetz *et al.*, 2011). Species were analysed separately to prevent any bias in terms of species differences in behaviour. All statistical analyses were 2-tailed with an alpha level of 0.05.

3.0 Results

In total, 6 hours of data were collected per individual over the study period. Results were relatively consistent across species.

3.1 Emperor Tamarins

Table 4 displays all statistical results for FRE and CE. FRE spent significantly more time 'not visible' than CE, who spent significantly more time in their shed. Natural substrates were used significantly more by FRE but no significant difference was found for use of artificial substrates.
Locomotion was significantly higher for FRE, specifically leaping, running, jumping and walking. No significant differences were found for hang or climb behaviour, although hanging was the only locomotory type exhibited more by CE. Foraging, rest, provisioned feeding and social behaviour were significantly higher in CE. Both affiliative and agonistic interactions were significantly higher in CE. No significant differences were found between conditions in stationary, natural feed or groom behaviours, although stationary behaviour was approaching significance, with more observed in CE.

Alarm calls were exhibited significantly more by FRE, but no significant differences were found for long calling or scent marking.

Use of horizontal, diagonal and vertical substrates was not significantly different between conditions. FRE used substrates of 2-10 cm significantly more, with use of 10-30 cm substrates significantly higher in CE. No significant differences were found for <2 cm and >30 cm diameter substrates. Neither group was recorded using the ground. Areas 2-5 m above ground were used significantly more by CE, but ground-2 m was not significantly different. Only FRE had access to heights of '>5 m', using these at a mean rate of 0.15±0.03 per hour. FRE spent significantly less time in 'contact' than CE, but 'proximity' was significantly higher. There was no significant difference found for 'distant' between groups.

3.2 Pied Tamarins

Table 5 displays all statistical results for FRP and CP. As with FRE, FRP were 'not visible' significantly more than CP, who spent significantly more time in their shed. Use of natural substrates was significantly higher for FRP, but artificial substrate use was not significantly different.

Locomotion was significantly higher in FRP, specifically leaping and running. No significant differences were found for jump, walk, hang or climb. Again, hanging was the only locomotory type exhibited more by CP. Grooming behaviour was significantly lower in FRP. There were no significant differences found for stationary, provisioned feed, natural feed, forage, rest, sexual or 'other' behaviour, although sexual behaviour was approaching significance. Affiliative interactions were significantly higher in CP but agonistic interactions were not significantly different between groups. Long calls were exhibited significantly more by FRP; no significant differences were found between conditions for alarm calling or scent marking.

Use of horizontal, diagonal and vertical substrates was not significant between conditions. Substrates of diameter '<2 cm' and '>30 cm' were used significantly more by FRP; substrates of 2-10 cm and 10-30 cm were used significantly more by CP. Use of the ground was rare for both groups, with no significant differences found. CP used ground-2 m significantly more than FRP, whereas FRP used 2-5 m significantly more. Heights of '>5 m' above ground were used at a mean rate of 0.12±0.03 per hour by FRP. CP spent time in 'contact' with their conspecifics significantly more than FRP, with time spent 'distant' significantly higher in FRP. No significant difference was found for 'proximity' between groups.

4.0 Discussion

Wild individuals must possess a repertoire of behaviours required for survival, including orientation and locomotion skills; feeding and foraging; obtaining suitable places to rest and sleep; and interspecific and intraspecific interaction (Box, 1991). The main reason for the initial reintroduction failure of golden lion tamarins was their inability to find food and move on natural substrates (Kleiman *et al.*, 1990). Encouragingly, all FRT and CT in this study exhibited natural behaviours, but mean rates of behaviour differed between conditions. FRT displayed mean rates of behaviour more similar to those of their wild counterparts, e,g, increased use of naturalistic substrates, locomotion types and appropriate communication. CT exhibited higher rates of intraspecific interaction and time spent in contact. Caged exhibits, although large and well-furnished, still offered fewer opportunities than the free-ranging exhibit.

4.1 Activity and environment use

FRT spent just over half the time not visible, predominantly in dense vegetation. This is typical of callitrichids housed in larger, more naturalistic exhibits (Chamove and Rohrhuber, 1989; Burrell and Altman, 2006) and in the wild (Digby, 1995), where they are extremely vulnerable to predators and dense vegetation provides them with cover (Garber, 1984; Chamove and Rohrhuber, 1989; Chamove, 1996). CT spent significantly more time in their sheds, especially during bouts of cold/rainy weather, when FRT would typically use natural shelter, displaying adaptability to unpredictable conditions.

Wild tamarins defend home ranges of 10-100 ha (Mittermeier *et al.*, 2008), and average daily travel distances of 1.5–2 km have been recorded (Garber. *et al*, 1993; Raboy and Dietz, 2004; Terborgh, 1983),. Locomotion was significantly higher in the free-ranging habitat, equating to approximately a third of overall activity: similar to the 33% documented in wild golden-lion tamarins (Dietz *et al.*,1997) and golden-headed lion tamarins (Raboy and Dietz, 2004), and higher than the 20-21% reported for emperor and saddle-back tamarins by Terborgh (1983). Considering that the need to search for resources is reduced in captivity, this is particularly encouraging. Quadruple progression and leaping are the predominant forms of travel in wild tamarins (Garber, 1980; Stafford *et al.*, 1994); quadruple walking was the main form of locomotion for all groups in this study. Running and leaping were significantly higher in all FRT; jumping and walking were also significantly higher in FRE. Whilst this demonstrates that FRT are capable of a range of locomotor types, mean rates were still lower than their wild counterparts. For example, although significantly higher in FRT, mean rates of leaping were still substantially lower than the 30% of travel documented in wild tamarins (Garber and Pruetz, 1994; Youlatos, 1999). Thus, motivation to leap could be explored. Spatial restrictions imposed by cages limited opportunities for continual running.

Feeding and foraging rates in wild tamarins range between 12.8% and 30% (Egler,1992; Keuroghlian and Passos, 2001; Raboy and Dietz, 2004). The highest combined feeding and foraging rate for tamarins in this study was approximately 11% of total activity. Again, as natural food acquisition and consumption in captivity is non-essential, lower rates were to be expected. Interestingly, foraging was higher in CE than any other group, in contrast to published findings on other primates (Chang *et al.*, 1999; Little and Sommer, 2002). However, Garber (1980) found that wild callitrichids often feed and forage in dense vegetation, so these behaviours may have been missed when FRT were not visible.

FRT in this study were observed foraging from fruiting trees and stalking moorhens, demonstrating their ability to successfully acquire natural foods.

Resting behaviour was significantly higher in CE, but was seldom observed in any group, and was lowest in FRT. Melfi and Feistner (2002) found that an increase in enclosure size was inversely related to the frequency of resting behaviour in Sulawesi macaques. Furthermore, we assume that most resting behaviour occurred when tamarins were not visible in dense vegetation and during the night, consistent with wild tamarins (Rylands and Mittermeier, 2008). Stationary behaviour was the most frequently recorded behaviour for all groups, consistent with other captive species housed in naturalistic environments (Price, 1992).

FRT used natural substrates significantly more than CT, including use of more varied substrate types in terms of diameter and orientation, consistent with findings on callitrichids in naturalistic environments and in the wild (Price *et al.*, 1992; Moore, 1997; Beck *et al.*, 2002; Stoinski and Beck, 2004). Wild pied tamarins typically use the middle-to-lower levels of the canopy, feeding on plants at heights of 10-12 m and animal prey at heights of 4-5 m (Egler, 1992; Vidal and Cintra, 2006). Wild emperor tamarins also avoid the highest levels of the canopy, feeding predominantly at 11-30 m (Terborgh, 1983). CT were restricted to heights of around 4 m; FRT were occasionally observed at heights above 5 m but were most commonly recorded at 2-5 m, which included shed entrances. In times of food scarcity, wild tamarins have been observed ground foraging, but for minimal time periods due to ground predators (Redshaw and Mallinson, 1991; Vidal and Cintra, 2006). Only pied tamarins were observed using the ground and did so solely to forage, consistent with wild behavioural patterns.

Although this competent environment use is reassuring, several comparable studies on wild callitrichids have concluded that certain locomotor and behaviour patterns are exhibited in association with specific substrate structures (Garber, 1984; Garber and Pruetz, 1994; Stafford *et al.*, 1994; Vidal and Cintra, 2006). Natural substrates were much more available in the free-ranging exhibits, whilst artificial perches (10-30 cm in diameter) were frequently provided in the cages and were often used for stationary and social behaviour. Furthermore, much of the basic structure of cages was composed of mesh, which probably resulted in increased hanging behaviour, as found by Chamove (2005). The placement of substrates within exhibits may also influence their use, e.g. ropes (2-10cm in diameter) were used to connect shed areas to surrounding trees in the free-ranging exhibits, necessitating their use.

4.2 Social interactions

Affiliative interactions were significantly lower in FRT, with agonistic interactions also significantly lower in FRE. Such decreased social interactions have been attributed to increased behavioural and spatial opportunities in larger, naturalistic exhibits (Box and Rohrhuber, 1993; Beck *et al.*, 2002; Melfi and Feistner, 2002). This is corroborated by the increased inter-individual distances found in FRT compared to CT in this study, as well as in other captive species (Box and Rohrhuber, 1993; Chang *et al.*, 1999; Little and Sommer, 2002) and wild tamarins (Norconk,1990).

All agonistic interactions recorded in FRT were interspecific, as commonly found *in situ* (Heymann and Buchanan-Smith, 2000). Territorial behaviour is essential to survival in the wild (Peres, 1989) and thus, agonistic interactions are to be expected, particularly as pied tamarins are not naturally sympatric with other callitrichids. However, wild emperor tamarins do form mixed-species associations with saddle-back tamarins, so these agonistic interactions with FRP are interesting. The significant occurrence of long-calls in FRP could indicate their use as territorial signals towards the FRE, as found for wild tamarins (Garber *et al.*, 1993; Windfelder, 2001).

Encouragingly, alarm calls were observed in all individuals in response to aerial predators and/or unfamiliar stimuli, although at lower rates than those observed in wild tamarins by Heymann (1990).

In captivity, natural predators and threats are less frequent and the consistent occurrence of some threats, e.g. humans, may cause habituation. FRE exhibited alarm calls significantly more than CE, potentially as a result of encountering more stimuli, as also found for cotton-top tamarins (Price *et al.*, 1991). Garber *et al.* (1993) reported that wild tamarins often exhibit alarm calls alongside aggressive encounters with other species; again, it is possible that the significant occurrence of alarm calls in FRE was attributable to the presence of FRP.

Scent-marking is essential in communicating information in callitrichids, including reproductive status, individual information and home ranges (Wormell and Feistner, 1992; Miller *et al.*, 2003), but its role in territory marking is disputed (Heymann, 2000; Gosling and Roberts, 2001; Miller *et al.*, 2003). FRT exhibited higher scent marking than CT, which appeared to increase during aggressive encounters, consistent with findings on wild moustached tamarins (Garber *et al.*, 1993).

4.3 Implications for conservation

A free-ranging exhibit appears conducive to the development of essential survival skills, including natural foraging, orientation in a 3-dimensional habitat and appropriate intra- and interspecific interactions, highlighting its value as a pre-release training ground for potential reintroduction candidates. A black lion tamarin reintroduced after two years of free-ranging experience at Durrell Wildlife Park, exhibited appropriate foraging and locomotor behaviour in the period following release (Valladares-Padua *et al.*, 2000). Stoinski and Beck (2004) also report that released animals with free-ranging experience 'nearly fell' less frequently and spent more time micro-manipulating than animals without such experience. They recommend placing tamarins into complex environments early in development to promote natural behaviours and increase survival opportunities after release. In this regard, free-ranging exhibits could play a role in the selection of potential reintroduction candidates based on evaluation of skills possessed (Beck *et al.*, 2002; Mathews *et al.*, 2005; Price *et al.*, 2012) and enable the time required to acquire various behaviours to be assessed (Stoinski *et al.*, 2003).

Whilst this study suggests that free-ranging exhibits can promote and preserve natural behaviours, it also supports Beck *et al.* (2002) in indicating that a free-ranging exhibit alone is not sufficient to replicate the challenges faced by wild animals. Valladares-Padua *et al.*, (2000) highlight the need for effective anti-predator avoidance skills, which are often noticeably lacking in captive individuals (Beck *et al.*, 1991). The benefits of pre-release training for predator avoidance have been documented across a range of captive species (van Heezik *et al.*, 1999; Shier and Owings, 2006; Moseby *et al.*, 2012), and thus, opportunities to refine specific skill sets prior to reintroduction attempts would optimise the chances of survival. For example, availability and placement of natural substrates in exhibits should promote the development and exhibition of a varied locomotor and behavioural repertoire (Stafford *et al.*, 1994; Boere, 2001).

5.0 Conclusions

Both captive exhibits provided opportunities for expression of natural behaviour. The free-ranging exhibit was conducive to the exhibition of behavioural skills that were dependent on the opportunities offered by the physical environment. The ability to express natural behaviour is generally considered beneficial to conservation in terms of increased individual psychological and physiological health and welfare, reintroduction success, education and research. However, divergence from wild tamarins was still evident in some aspects of behaviour in both exhibit types. To further promote natural behaviours, all tamarins should be provided with additional behavioural opportunities to ensure the acquisition and practice of desirable skills, such as anti-predator avoidance and manipulation of substrate types within exhibits. Longitudinal studies on a range of species would be valuable in assessing the impact of free-ranging exhibits in zoos and other institutions.

6.0 Conflict of interest

The author and co-authors of this manuscript have no conflict of interest, real or perceived.

7.0 Acknowledgments

Many thanks go to the keeping staff at Durrell Wildlife Park for being so accommodating and informative.

8.0 References

Armstrong, D., and Santymire, R., 2013. Hormonal and behavioral variation in pied tamarins housed in different management conditions. *Zoo Biol.* **32** (3), 299-306.

Beck, B. B., Kleiman, D. G., Dietz, J. M., Castro, I., Carvalho, C., Martins, A., and Rettberg-Beck, B. (1991). Losses and reproduction in reintroduced golden lion tamarins Leontopithecus rosalia. *Dodo.* ***27***, 50-61.

Beck, B., Castro, M., Stoinski, T. and Ballou, J., 2002. The effects of prerelease environments and postrelease management on survivorship in reintroduced golden lion tamarins. *In*: Kleiman, D. G. and Rylands, A. B. *Lion Tamarins: Biology and Conservation*, 283-300.

Boere, V., 2001. Environmental enrichment for neotropical primates in captivity. *Ciência Rural.* **31** (3), 543-551.

Box, H.O., and Rohrhuber, B., 1993. Differences in behaviour among adult male, female pairs of cotton-top tamarins (*Saguinus oedipus*) in different conditions of housing. *Animal Technology*. **44**, 19-19.

Box, H., 1991. Training for life after release: simian primates as examples. *In: Symposia of the Zoological Society of London*, pp. 111-123.

Burrell, A.M., and Altman, J.D., 2006. The effect of the captive environment on activity of captive cotton-top tamarins (*Saguinus oedipus*). *J App Anim Welf Sci.* **9** (4), 269-276.

Chamove, A. S., 1996. Predator (*Mustela nivalis*) responses in captive-bred *Callithrix jacchus*. *Neotropical Primates*. **4,** 56-57

Chamove, A.S., 2005. Environmental enrichment for monkeys using plants. *Laboratory Primate Newsletter.* **489** (493), 1.

Chamove, A.S., and Rohrhuber, B., 1989. Moving callitrichid monkeys from cages to outside areas. *Zoo Biol.* **8** (2), 151-163.

Chang, T.R., Forthman, D.L. and Maple, T.L., 1999. Comparison of confined mandrill (*Mandrillus sphinx*) behavior in traditional and “ecologically representative” exhibits. *Zoo Biol.* **18** (3), 163-176.

Davey, G., 2006. Relationships between exhibit naturalism, animal visibility and visitor interest in a Chinese zoo. *Appl Anim Behav Sci.* **96** (1), 93-102.

Dietz, J. M., Peres, C. A., and Pinder, L., 1997. Foraging ecology and use of space in wild golden lion tamarins (Leontopithecus rosalia). *Am J Primatol.* ***41***, 289-305.

Digby, L. J., 1995. Social organization in a wild population of Callithrix jacchus: II. Intragroup social behavior. *Primates*. **36** (3), 361-375.

Egler, S., 1992. Feeding ecology of *Saguinus bicolor bicolor* (Callitrichidae: Primates) in a relict forest in Manaus, Brazilian Amazonia. *Folia Primatol*, **59** (2), 61-76.

Fàbregas, M.C., Guillén- Salazar, F. and Garcés- Narro, C., 2012. Do naturalistic enclosures provide suitable environments for zoo animals? *Zoo Biol.* **31** (3), 362-373.

Garber, P. A., 1980. Locomotor behavior and feeding ecology of the Panamanian tamarin (Saguinus oedipus geoffroyi, Callitrichidae, Primates). *Int J Primatol. 1*(2), 185-201.

Garber, P. A., 1984. Use of habitat and positional behaviour in a neotropical primate, *Saguinus oedipus*. *In:* P. S. Rodman & J. G. H. Cant (Eds.), *Adaptations for foraging in nonhuman primates: Contributions to an organismal biology of prosimians, monkeys, and apes.* 112-133. New York: Columbia University Press.

Garber, P. A., Pruetz, J. D., and Isaacson, J., 1993. Patterns of range use, range defense, and intergroup spacing in moustached tamarin monkeys (Saguinus mystax). *Primates*. **34** (1), 11-25.

Garber, P., and Pruetz, J., 1994. Positional behavior in moustached tamarin monkeys: effects of habitat on locomotor variability and locomotor stability. *J Hum Evol.* **28** (5), 411-426.

Gosling, L., and Roberts, S., 2001. Testing ideas about the function of scent marks in territories from spatial patterns. *Anim Behav.* **62** (3), F7-F10.

Heymann, E. W., 1990. Interspecific relations in a mixed-species troop of moustached tamarins, *Saguinus mystax*, and saddle-back tamarins, *Saguinus fuscicollis* (Primates: Callitrichidae), at the Rio Blanco, Peruvian Amazonia. *Am J Primatol.* **21**, 115-127.

Heymann, E. W., and Buchanan-smith, H. M., 2000. The behavioural ecology of mixed- species troops of callitrichine primates. *Biol Rev.* **75** (2), 169-190.

Hosey, G.R., 2005. How does the zoo environment affect the behaviour of captive primates? *Appl Anim Behav Sci.* **90** (2), 107-129.

Hosey, G., Melfi, V. and Pankhurst, S., 2009. *Zoo animals: behaviour, management and welfare.* Oxford: Oxford University Press.

Keuroghlian, A., and Passos, F. C., 2001. Prey foraging behavior, seasonality and time-budgets in black lion tamarins, Leontopithecus chrysopygus (Mikan 1823) (Mammalia, Callitrichidae). *Braz J Biol.* **61** (3), 455-459.

Kleiman, D. G., Beck, B. B., Baker, A. J., Ballou, J. D., Dietz, L. A. and Dietz, J. M., 1990: The conservation program for the golden lion tamarin *Leontopithecus rosalia*. Endangered Species Update 08, 82—85.

Little, K.A., and Sommer, V., 2002. Change of enclosure in langur monkeys: implications for the evaluation of environmental enrichment. *Zoo Biol.* **21** (6), 549-559.

Mallapur, A., Qureshi, Q. and Chellam, R., 2002. Enclosure design and space utilization by Indian leopards (*Panthera pardus*) in four zoos in southern India. *J App Anim Welf Sci.* **5** (2), 111-124.

Maple, T.L., and Finlay, T.W., 1989. Applied primatology in the modern zoo. *Zoo Biol.* **8** (S1), 101-116.

Martin, P. R., Bateson, P. P. G., and Bateson, P., 1993. *Measuring behaviour: an introductory guide*. Cambridge University Press.

Mathews, F., Orros, M., McLaren, G., Gelling, M. and Foster, R., 2005. Keeping fit on the ark: assessing the suitability of captive-bred animals for release. *Biol Conserv.* **121** (4), 569-577.

McPhee, M.E., and Carlstead, K., 2010. The importance of maintaining natural behaviors in captive mammals. *In:* Kleiman *et al.*, 2010. *Wild Mammals in Captivity: Principles and Techniques for Zoo Management (2nd Ed).Chicago: University of Chicago Press,* 303-313.

Melfi, V., and Feistner, A., 2002. A comparison of the activity budgets of wild and captive Sulawesi crested black macaques (*Macaca nigra*). *Anim Welf.* **11** (2), 213-222.

Melfi, V.A., McCormick, W. and Gibbs, A., 2004. A preliminary assessment of how zoo visitors evaluate animal welfare according to enclosure style and the expression of behavior. *Anthrozoos.* **17** (2), 98-108.

Miller, B., Biggins, D., Wemmer, C., Powell, R., Calvo, L., Hanebury, L., and Wharton, T., 1990. Development of survival skills in captive-raised Siberian polecats (Mustela eversmanni) II: predator avoidance. *J Ethol.* **8** (2), 95-104.

Miller, K.E., Laszlo, K. and Dietz, J.M., 2003. The role of scent marking in the social communication of wild golden lion tamarins, *Leontopithecus rosalia*. *Anim Behav,* **65** (4), 795-803.

Mittermeier, R.A., Boubli, J.-P., Subirá, R. and Rylands, A.B., 2008. *Saguinus bicolor*. In: IUCN 2014. IUCN Red List of Threatened Species. Version 2014.1. <www.iucnredlist.org>. Downloaded on 20th June 2014.

Moore, M., 1997. Behavioural adaptation of captive-born silvery marmosets *Callithrix argentata argentata* to a free-ranging environment. *Dodo, J. Jersey Wildl Preserv Trust.* **33**, 155-155.

Morgan, K.N., and Tromborg, C.T., 2007. Sources of stress in captivity. *Appl Anim Behav Sci.* **102** (3), 262-302.

Moseby, K. E., Cameron, A., and Crisp, H. A., 2012. Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia?. *Anim Behav. **83*** (4), 1011-1021.

Norconk, M.A., 1990. Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. *Am J Primatol.* **21** (2), 159-170.

Peres, C.A., 1989. Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. *Behav Ecol Sociobiol.* **25** (3), 227-233.

Prescott, M. J., and Buchanan-Smith, H. M., 2004. Cage sizes for tamarins in the laboratory. *Anim Welf.* **13**, 151-157.

Price, E.C., 1992. Adaptation of captive-bred cotton-top tamarins (*Saguinus oedipus*) to a natural environment. *Zoo Biol.* **11** (2), 107-120.

Price, E. C., Feistner, A. T. C., Caroll, J. B., and Young, J. A., 1989. Establishment of a free-ranging group of cotton-top tamarins (*Saguinus oedipus*) at Jersey Wildlife Preservation Trust. *Dodo.* **26,** 60-69.

Price, E. C., McGivern, A. M., and Ashmore, L., 1991. Vigilance in a group of free- ranging

25 cotton-top tamarins *Saguinus oedipus*. *Dodo.* **27,** 41-49.

Price, E., Wormell, D., Brayshaw, M., Furrer, S., Heer, T. and Steinmetz, H., 2012. Managing free-ranging callitrichids in zoos. *International Zoo Yearbook.* **46** (1), 123-136.

Raboy, B. E., and Dietz, J. M., 2004. Diet, foraging, and use of space in wild golden- headed lion tamarins. *Am J Primatol.* **63** (1), 1-15.

Redshaw, M.E., and Mallinson, J.J., 1991. Stimulation of natural patterns of behaviour: Studies with golden lion tamarins and gorillas. *In:* Box, H. *Primate responses to environmental change.* Springer, 1991, pp. 217-238.

Rylands, A.B. and Mittermeier, R.A., 2008. *Saguinus imperator ssp. subgrisescens*. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org>. Downloaded on 17th September 2014.

Shepherdson, D., 1994. The role of environmental enrichment in the captive breeding and reintroduction of endangered species. *In:* Olney, P.J.S, *et al. Creative Conservation: Interactive management of wild and captive animals.* Springer, 1994, pp. 167-177.

Shepherdson, D.J., Mellen, J.D. and Hutchins, M., 1998. *Second nature: environmental enrichment for captive animals.* Smithsonian Institution Press.

Shier, D. M., and Owings, D. H., 2006. Effects of predator training on behavior and post-release survival of captive prairie dogs (*Cynomys ludovicianus*). *Biol Conserv.* ***132*** (1), 126-135.

Stafford, B.J., Rosenberger, A.L. and Beck, B.B., 1994. Locomotion of free- ranging golden lion tamarins (*Leontopithecus rosalia*) at the National Zoological Park. *Zoo Biol.* **13** (4), 333-344.

Steinmetz, H., Zingg, R., Ossent, P., Eulenberger, U., Clauss, M. and Hatt, J., 2011. Comparison of indoor and captive, free-roaming management in golden-headed lion tamarins (*Leontopithecus chrysomelas*) at Zürich Zoo. *Anim Welf.* **20** (2), 205-210.

Stoinski, T., Beck, B., Bloomsmith, M. and Maple, T., 2003. A behavioral comparison of captive-born, reintroduced golden lion tamarins and their wild-born offspring. *Behaviour.* **140** (2), 137-160.

Stoinski, T., and Beck, B., 2004. Changes in locomotor and foraging skills in captive- born, reintroduced golden lion tamarins (*Leontopithecus rosalia rosalia*). *Am J Primatol.,* **62** (1), 1-13.

Terborgh, J., 1983. *Five New World Primates.* Cambridge University Press.

Valladares-Padua, C., Martins, C. S., Wormell, D., and Setz, E. Z. F., 2000. Preliminary evaluation of the reintroduction of a mixed wild-captive group of black lion tamarins *Leontopithecus chrysopygus*. *Dodo.* **36**, 30-38.

van Heezik, Y., Seddon, P. J., and Maloney, R. F., 1999. Helping reintroduced houbara bustards avoid predation: effective anti-predator training and the predictive value of pre-release behaviour. *Anim Conserv.* **2** (3), 155-163.

Vidal, M.D., and Cintra, R., 2006. Effects of forest structure components on the occurence, group size and density of groups of bare-face tamarin (*Saguinus bicolor*-primates: Callitrichinae) in Central Amazonia. *Acta Amazonica.* **36** (2), 237-248.

Williams, S.E., and Hoffman, E.A., 2009. Minimizing genetic adaptation in captive breeding programs: a review. *Biol Conserv.* **142** (11), 2388-2400.

Windfelder, T.L., 2001. Interspecific communication in mixed-species groups of tamarins: evidence from playback experiments. *Anim Behav.* **61** (6), 1193-1201.

Wormell, D., 2000. Management guidelines for pied tamarins *Saguinus bicolor bicolor*. *Dodo.* **36**, 87-87.

Wormell, D., 2010. Diet for callitrichids at Durrell Wildlife Conservation Trust. *In:* Bairrão Ruivo, E. *EAZA Husbandry Guidelines for Callitrichidae – 2nd Edition.* EAZA, Amsterdam, p. 109.

Wormell, D., Brayshaw, M., Price, E. and Herron, S., 1996. Pied tamarins *Saguinus bicolor bicolor* at the Jersey Wildlife Preservation Trust: management, behaviour and reproduction. *Dodo.* **32**, 76-97.

Wormell, D., and Feistner, A.T., 1992. Preliminary observations of scent marking in captive pied tamarins *Saguinus bicolor bicolor*. *Dodo.* **28,** 70-77.

Youlatos, D., 1999. Comparative locomotion of six sympatric primates in Ecuador. *In: Annales des Sciences Naturelles-Zoologie et Biologie Animale,* Elsevier. pp. 161-168.

Tables

***Table 1**: Details of all study subjects*

** FRE: Free-ranging emperors; FRP: Free-ranging pieds; CE: Caged emperors; CP: Caged pieds*

***Table 2:** A comparison of exhibit types used in this study.*

***Table 3:** An ethogram of behaviours for all tamarins in the study, adapted from Price (1992), Stafford et al. (1994), Wormell et al. (1996) and Armstrong and Santymire (2013).*

***Table 4**: Mean rate per hour (±SE), sampling method, z values and statistical significance of behaviours exhibited by free-ranging (N=4) and caged (N=4) emperor tamarins. P values are for 2-tailed, Mann-Whitney U tests. Significant values (P < 0.05) are in bold.*

***Table 5**: Mean rate per hour (±SE), sampling method, z values and statistical significance of behaviours exhibited by free-ranging (N=2) and caged (N=6) pied tamarins. P values are for 2-tailed, Mann-Whitney U tests. Significant values (P<0.05) are in bold.*

Figures

***Figure 1:** Map of Durrell Wildlife Park showing the 'Tamarin Wood' area used by FRT and the location of the caged exhibits.*