

Mixed Species Exhibits in German Zoological Gardens (Part 2)

Special References on Primates

Cover photos:

Left: Female elephant inspecting male baboon (Safaripark Beekse Bergen; photo: R. Deleu). Right above: Starting interaction (obviously food related) between Lion-tailed macaques and Borneo Orangutan at the "zoORANGerie" Münster (Allwetterzoo Münster). Right down: Common marmoset (right) and Spix's black-manteled tamarin (left) in outdoor enclosure, also open for visitors (Zoologischer Garten Rostock).

Editor: Dr. Dr. Michael Schwibbe, Dr. Thomas Ziegler
Assistance: Heike Klensang
German Primate Center (DPZ)

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Foreword

The present 65 issue of Primate Report was edited to provide more detailed information on certain polyspecific associations of primates in captivity, a complex subject, already presented in Primate Report 64, which focused on Zoos in Germany.

Here, three international scientific articles are presented, describing special mixed species exhibits with primates involved in greater detail. Two of these articles present long-term experiences made in the Safaripark Beekse Bergen (baboons and elephants) and Belfast Zoo (several Callitrichid species), both also referring to data from the wild. The third article presents an experimental study on the consequences of mixing Howler monkeys and Tamarins to selected behavioural aspects under semi-free conditions in Panama.

A short introduction to the general background of the studies on mixed species exhibits, presented in Primate Report issue 64, and the present issue of Primate Report, is given here again.

We would like to thank the authors of the following articles for their contributions, which provide valuable information on a subject that still needs further studies in the wild and is becoming increasingly important for the management of animals in captivity.

Dr. Thomas Ziegler

BACKGROUND OF THE STUDY. ZIEGLER, T.

During the evolution of Zoos, from the mere presentation of animal collections, separately exhibited in single species cages, to the presentation of exhibits, set up to resemble natural habitats, the idea of mixing different species in the same enclosure became increasingly important.

Traditionally, many Zoos have considerable experience in the combination of numerous fish- reptile- and bird species in aquariums, reptile gardens or flight cages, but the concept of mixing two or more mammal species is relatively young. To a certain degree, the underlying reasons can be seen in the potential risks, technical demands and problems, that can be caused by establishing a new association of mammals in captivity.

Nevertheless, as polyspecific associations can be regularly observed in many sympatric animals including mammals in the wild, the concept of mixed species exhibits represents an important and promising measure to approximate natural conditions in captivity. Among vertebrates, stable polyspecific association are quite common and can be observed regularly in wild fish, birds, ungulates and primates (BERTRAM, 1978; TERBORGH, 1990; BUCHANAN-SMITH, 1990). The ultimate causes of this phenomenon can be seen in behavioural strategies to avoid predators and to optimise foraging ("Safety in numbers": TERBORGH, 1990; MORSE, 1970; GADDIS, 1980; POWELL, 1985; MUNN, 1986). Although not every species involved in a certain polyspecific association gains advantages equal in quantity or quality, the overall benefits of living in a mixed flock have to outweigh the potential costs for each individual, as polyspecific associations are evolutionary evolved strategies.

Many primate species are known to regularly form long term polyspecific associations in the wild (STRUHSAKER, 1981; POOK and POOK, 1982; GAUTIER-HION, 1988; HEYMANN, 1990). These associations can be formed within the taxonomic family or subfamily (e.g. Cebidae, Cercopithecidae, Callitrichinae) or between different taxonomic orders (e.g. primates & ungulates). Among Callitrichids (subfam.: Callitrichinae), the forming of polyspecific associations is already known as an integral part of their biology (HEYMANN and BUCHANAN-SMITH, 2000).

Against this background, polyspecific associations in captivity can be seen as a special enrichment, which leads to a more complex and thus more natural environment (HARDIE, 1996; HEYMANN et al., 1996), having positive effects for animals and visitors of these exhibits.

The possibility of exhibiting mammals of different species or combining mammals with bird or reptile species within the same enclosure can have several benefits on different levels. These benefits involve pure practical aspects, like alleviating cage space problems, educational aspect for the public (as long as the association considers the zoogeographic distribution of the species involved) and last but not least, aspects of behavioural and social enrichment for the animals, due to interspecific or intensified intraspecific interactions.

The practical advantages of mixed species exhibits has become more and more important during the last decades, as Zoos have become increasingly involved in European and International breeding programs for an increasing number of species that are critically endangered in their natural habitats. While the number of these species and the demand for breeding programs in captivity increases, space for suitable exhibits in Zoos is limited. Mixed species exhibits can alleviate this problem, as already available enclosures can serve to keep two or more species at a time without disadvantages for any of the species involved. On the contrary, the association of different species in mixed exhibits can often represent an environmental enrichment for the individuals involved and this holds true especially for primates. In general polyspecific associations, as an additional stimulus in captivity, can positively influence individual behavioural patterns and time budgets in terms of interspecific and intensified intraspecific interactions. The stimulation of such interactive behavioural patterns can be an important factor for the wellbeing of the animals (e.g. to avoid stereotypic behaviours), as time budgets for foraging and predator avoidance are drastically reduced in captivity.

This study was set up to support the exchange of expertise in establishing and maintaining mixed species exhibits in Zoos and other animal keeping facilities of Germany and abroad, as well as to promote the outstanding value of this concept for future animal keeping and - exhibition facilities.

EVALUATION OF THE MIXED-SPECIES EXHIBIT OF AFRICAN ELEPHANTS AND HAMADRYAS BABOONS IN SAFARI BEEKSE BERGEN, THE NETHERLANDS. DELEU, R., VEENHUIZEN, R. AND NELISSEN, M.

Key words: hamadryas baboon, African elephant, mixed-species exhibit, interspecific interactions, environmental enrichment, behavioural enrichment, cross-contamination

Abstract

Since 1994, hamadryas baboons (*Papio hamadryas hamadryas*) and African elephants (*Loxodonta africana*) are housed together in a 1.3 ha outdoor enclosure during daytime in Safari Beekse Bergen, the Netherlands. A detailed description and evaluation of the success of this mixed-species exhibit is presented. The only problem associated with the mixing of species was a one-off cross-contamination with salmonella. However if health of both species is closely monitored, the potential threat of cross-contamination cannot be considered as a major problem. Especially if this problem is weighed against the numerous advantages of the mixed exhibit: large enclosure for both species, environmental enrichment through frequent direct and indirect interspecific interactions, behavioural enrichment through promotion of species-specific behaviour and the development of special behaviour, the almost complete absence of stereotypic behaviour in both species and finally more educational and scientifically interesting exhibits.

Introduction

Mixed-species exhibits with mammals are more and more common in zoos. Most of the time primates, ungulates and/or birds are involved in these associations (THOMAS and MARUSKA, 1996). Baboons have been used frequently in successful mixed-species exhibits with ungulates, hyraxes and mongooses (CROTTY, 1981; THOMAS and MARUSKA, 1996). Recent examples include: gelada baboons (*Theropithecus gelada*), barbary sheep (*Ammotragus lervia*) and rock hyrax (*Procavia capensis*) in Wilhelma Zoologisch-Botanischer Garten in Stuttgart, Germany; hamadryas baboons (*Papio hamadryas hamadryas*) and barbary sheep in Amersfoort, the Netherlands; hamadryas baboons and Nubian ibex (*Capra ibex nubiana*) at Tierpark Hellabrunn in München, Germany; hybrid baboons (*Papio hamadryas hamadryas* x *Papio hamadryas anubis*), nilgai (*Boselaphus tragocamelus*) and zebra (*Equus burchelli*) in Knowsley Safari Park, U.K. Elephants are generally kept in separate enclosures, but can successfully be combined with other species if the latter have safe areas to get away from the elephants (STEVENSON, in press). However most experiments are recent and have been restricted to mixing elephants and ungulates: African elephants (*Loxodonta africana*), common elands (*Taurotragus oryx*) and oryx (*Oryx gazella*) in Parque de la Naturaleza de Cabárceno, Spain; African elephants, African buffalo (*Syncerus caffer*), ostrich (*Struthio camelus*), blesbok

(*Damaliscus pygargus phillipsi*), reticulated giraffe (*Giraffa camelopardalis reticulata*), and common eland in Borås Djurpark Zoo, Sweden; Asian elephants (*Elaphus maximus*), axis deer (*Axis axis*) and blackbucks (*Antilope cervicapra*) in Heidelberg, Germany.

In Safari Beekse Bergen in Hilvarenbeek, the Netherlands, African elephants are housed together with hamadryas baboons since 1994 (VAN VLIET, 1994) and this is the only existing mixed exhibit of elephants and primates to our knowledge at present. Hamadryas baboons live in semi deserts of countries at both sides of the Red Sea: Sudan, Eritrea, Ethiopia and Somalia in Africa and Saudi Arabia and Yemen in Asia (KUMMER, 1995). They have a multilevel fission-fusion society of which the one-male unit (OMU, consisting of one adult male, one or more females and their offspring) is the smallest subgroup (followed by clan, band and troop). A troop spends the night on a so-called sleeping rock and splits up into successively smaller units in the morning for foraging to reassemble again in the evening following the same pattern (KUMMER, 1995). Female African elephants live in family units with their offspring and several family units may join together to form a clan. Sometimes herds of hundreds of animals can be seen. Bulls leave their family unit shortly after sexual maturity and remain more or less solitary (MOSS, 2000). African elephants inhabit a wide range of habitats including semi deserts and there are relict populations of African elephants left in the all of the countries where hamadryas baboons live (BARNES et al., 1999). However, elephants are limited in number and status of both species is not completely known due to political instability in these countries, so it is not sure if hamadryas baboons and African elephants actually live sympatrically.

The goal of this article is to describe the aggregation of elephants and baboons in Safari Beekse Bergen in detail and to evaluate its success.

Enclosure

Baboons and elephants share an outdoor enclosure of about 13000 m² during daytime and are housed separately during the night in indoor enclosures. On days with temperature below zero degrees Celsius, baboons stay in their indoor cage or in a connected fenced outdoor enclosure during daytime as well to prevent them from escaping by crossing the frozen moat. Elephants can use the outdoor enclosure for short periods on these days, except when it is too icy.

The outdoor enclosure is a sand plain with a central rock formation, surrounded by a ca. 3.8 m wide and 0.75-1.8 m deep moat (Figure 1 and see VAN VLIET, 1994 for a more detailed description). About 25 pines (*Pinus sylvestris*) are scattered on the eastern side of the enclosure (the "forested part"). In the western part of the enclosure (the "open part") there are 2 quagmires. An artificial waterfall originates on top of the rocks and discharges in a large basin. This water basin is connected through a 0.15 m deep and 1.25 m wide overflow with the surrounding moat. Although the moat is wide and deep enough to prevent elephants and baboons from escaping, five horizontal electric wires prevent the elephants from destroying the moat construction. At the observation posts for visitors, these electric wires are hidden by rocks, but baboons can jump over the electric wires and use the rocks for foraging in the moat.

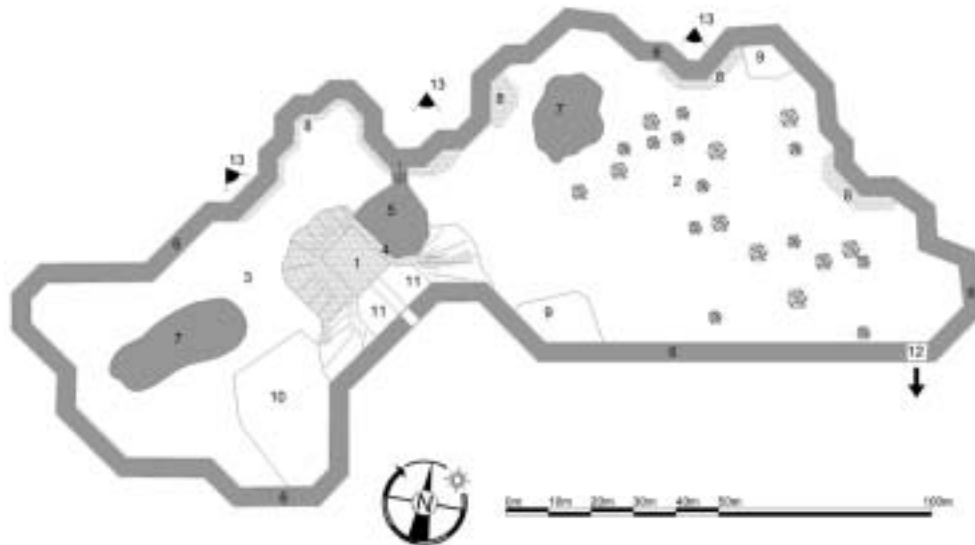


Fig. 1.: Ground plan of mixed outdoor enclosure of African elephants and hamadryas baboons in Safari Beekse Bergen, the Netherlands: (1) central rock formation under which indoor enclosure of baboons is hidden; (2) forested part with pines; (3) open part; (4) waterfall that discharges in (5) water basin with overflow to (6) surrounding moat; (7) quagmires; (8) rocks; (9) inaccessible area for elephants where grass and herbs grow; (10) feeding place of baboons; (11) fenced winter outdoor enclosure of baboons; (12) gate leading to indoor enclosure of elephants; (13) observation places for visitors (ground plan: T.O.P.office).

Several areas are inaccessible for the elephants. First, groups of pines are surrounded by a double horizontal electric wire (about 0.75 and 1.25 m high respectively). Initially, the pines were only protected by vertical electric wires stretched between two trunk rings, but the elephants quickly destroyed the wire construction and dug up the pine roots. After several pines were destroyed, it was decided that a more effective protection against elephants was needed. However, since baboons can still enter these areas and dig up the roots as well it is not certain if the pines are protected enough today. Secondly, two smaller parts of the enclosure with grass and herbs are surrounded by a 1.25 m high electric fence consisting of ten horizontal electric wires. Initially the fence was intended as protection against baboons as well to protect bamboo and trees in these areas. However, after a while the baboons dug up the sand under the lowest wire and occasionally crawled underneath or simply jumped over the fence using its piles for taking off. This soon resulted in the destruction of bamboo and trees. Grass and herbs can still grow in these parts today, because not all baboons enter them (mostly juveniles and subadults do, although a few OMUs also do it regularly). It has to be mentioned that planting has to be protected equally well in single-species exhibits of both species and that these problems with planting are consequently not related to the mixing of species. Third, the feeding

place of baboons is surrounded by a 0.75-1.0 m high electric wire to prevent the elephants from stealing food when baboons are fed.

During autumn and winter, a larger part of the enclosure (with one quagmire and the basin) and the second quagmire is inaccessible for the elephants to prevent them from bathing when temperature is too low. This is done by using horizontal electric wires of about 0.75 m high: one between the eastern boundary of the central rock formation and the surrounding moat at the opposite side of the enclosure and one around the second quagmire.

Group composition and demography

Hamadryas baboons and African elephants were introduced in the new enclosure in 1994. The five female African elephants were wildborn in Zimbabwe and came to Safari Beekse Bergen in 1988 at the estimated age of 1 to 2 years old (Table 1) after being taken into captivity when the rest of their herd was culled. The baboons came as a group to Safari Beekse Bergen in December 1993 from the former Windsor Safaripark in the UK, where they were also kept in a mixed exhibit with barbary sheep and lappet-faced vultures (*Torgos tracheliotus*). At that time the group consisted of 58 animals: 24 males (6 adults, 4 subadults, 9 juveniles and 3 infants), 33 females (20 adults, 3 subadults, 9 juveniles and 1 infant) and 1 infant of unknown sex. There were 5 OMUs (with 1, 2, 3, 4 and 10 females respectively) and 1 adult bachelor male. Most baboons were captive born in Windsor Safaripark (only 9 baboons were born in other locations) and no new animals had been introduced in the group since more than 20 years (data based on zoological records from Windsor Safaripark).

Table 1: Group composition of African elephants in Safari Beekse Bergen, the Netherlands in August 2002 (exact birth dates are unknown since all elephants were wildborn in Zimbabwe).

Name	Sex	Estimated birth month
Carla	female	June 1987
Erna	female	January 1987
Linda	female	January 1987
Olga	female	January 1987
Shiba	female	June 1986

After arriving in Safari Beekse Bergen, the baboons were kept in their indoor enclosure for a while to adjust to their new environment. After a few days, they were introduced in the outdoor enclosure. The baboons immediately explored the entire enclosure and when they were familiar with it some days later, the elephants were introduced as well. Initially, baboons and elephants were afraid of each other, but the elephants had overcome their fear by the next day while it took the baboons a bit longer. The elephants initially stayed in the forested part of the enclosure (close to the gate that leads to their indoor enclosure) and it took about two months before four of the elephants dared to cross the overflow from the basin to the moat to explore the plain part of the enclosure. One elephant has not dared to cross the overflow till now.

No demographic changes occurred in the elephant group, since all five of them are still alive and there is no male to reproduce. However, there are plans to bring a young bull to the park to start breeding (this bull will be kept in a separate enclosure and females will be introduced to him when one or more of them are in oestrus). In the baboon group there have been a lot of demographic changes. Initially, all but two newborn infants died shortly after birth. The cause of death could not be determined since most of the time the infants were partly cannibalised and consequently autopsy was impossible. However, infanticide cannot be excluded since rough handling of infants by males was frequently observed. Although the level of infant mortality remained high, the baboons started to reproduce more and more successfully and their number rose very quickly to about 75 animals, so birth control measures were needed. In 1996, the first 26 females were sterilised (for details see KAANDORP and VERVEST, 1997). Despite this intervention and the fact that several animals died over the years of various causes (*Salmonella*-infection, see below; *Trichuris*-infection; age; drowning) the number of baboons was still rising too quickly and in spring 2000 another 11 females were sterilised. At the end of 2000, there was a lot of fighting between the males because of the high number of bachelor adult and subadult males in the group attempting to establish their OMU. The removal (and euthanasia) of 2 adult and 8 subadult males restored group stability. Today, the group consists of 61 baboons: 36 females (32 adult, 2 subadult and 2 juveniles) of which 25 females are sterilised and 25 males (13 adult, 3 subadult, 6 juveniles and 3 infants). There are two adult bachelor males, eleven OMU's (with 2 to 6 females per male) and probably four clans, but the latter are difficult to distinguish (Table 2).

Table 2: Adult males and composition of one-male units (n = 11) and supposed clans of the hamadryas baboon group in Safari Beekse Bergen, the Netherlands in August 2002. Numbers between brackets are numbers of subadult females that are not yet fully attached to a male, but spend a lot of time with the corresponding male.

Clans	Adult Males	Number of females	Sterilised females	Fertile females
A	Largo	6	2	4
	Zorro	2	2	0
	Novo	0	0	0
B	Gumo	3	3	0
	Tango	3	3	0
	Salvo	2	2	0
C	Vipo	4	2	2
	Wempo	3 (1)	2	1 (1)
	Ampo	2 (1)	2	0 (1)
	Jero	2	2	0
D	Euro	3	3	0
	Kondo	2	2	0
	Castro	0	0	0
4	13	32 (2)	25	7 (2)

Management

Before both species can leave their respective indoor enclosures, keepers put hay and sometimes birch or other branches for the elephants in the forested part of the outdoor enclosure. To prevent the baboons from escaping while the elephants enter the outdoor enclosure, the latter are let out before the baboons (and conversely baboons are let in before the elephants in the evening). Immediately afterwards, baboons get breakfast (apples, carrots, onions, cabbage and pellets) in the plain part of the enclosure. The elephants are fed (apples, cabbage, carrots and pellets) two more times in the outdoor enclosure during the day near the gate leading to their indoor cages. Indoor enclosures of both species are cleaned. Because baboons get their main meal in the evening (apples, bread, cabbage, carrots, onions and pellets), they can be lured inside easily. After elephants are put in their indoor enclosure and fed once again (apples, cabbage, carrots, oats and pellets), keepers remove the bulk of elephant dung from the outdoor enclosure. No other regular cleaning of the outdoor enclosure is necessary.

Because baboons and elephants were used to keepers entering their enclosure before, the keepers can enter the outdoor enclosure without problems if necessary (e.g. when people throw potentially dangerous items in the enclosure or when electric wires need to be fixed).

Problems associated with the mixing of species

Feeding

Although interspecific feeding competition is limited because baboons and elephants are fed separately in the outdoor enclosure and receive their main meal in the evening in the indoor enclosures, there were some problems with feeding competition in the beginning. When baboons were fed breakfast, elephants successfully chased the baboons away and stole their food. To solve this problem, the baboons' feeding place was surrounded by an electric wire. This should make it possible for the baboons to eat in peace (and should give them an additional opportunity to stay out of the elephants' reach during the rest of the day). However when elephants approach the feeding place, baboons still flee to the rocks and wait till the elephants leave to return. The food baboons drop in their flight is quickly eaten by the elephants, but baboons get by far the greatest part. In addition, elephants search for leftovers between the rocks with their trunks, alarming the baboons and making them flee to the top of the rocks. Alternatively, when elephants were fed some baboons (mostly adult males) successfully stole food. Although elephants were able to chase baboons away, the latter outnumbered them by far and an important part of their food was stolen. To prevent this, the keepers now stay in the neighbourhood until the elephants have finished eating to deter baboons if necessary. Fortunately, the elephants consume their food very quickly!

Health

Until now there have been no accidents related to the mixed-species exhibit, but in September 1999 there was a cross-contamination with *Salmonella typhimurium* (see HUBER and KAANDORP, in press, for a detailed description). The incident

started with the observation that the baboons were coughing (which was later diagnosed as bronchitis caused by *Bordetella bronchiseptica*). In spite of antibiotic treatment, the baboons kept coughing and one week later started to lack appetite. Different animals had developed diarrhoea. Three weak, anorectic and cachexic baboons were euthanised and sent to pathology (one juvenile female, one juvenile male and one adult male). In the next days the elephants started to lack appetite as well and some of them were even lethargic. One juvenile male baboon died. As soon as the autopsy results of the euthanised baboons were known (salmonellosis), baboons and elephants were kept separately in their respective indoor enclosures and promptly treated with antibiotics. Elephants were treated as well because *Salmonella typhimurium* is not species-specific. Later isolation of *Salmonella typhimurium* from dung of one elephant confirmed suspicions of salmonellosis in elephants. In addition to the antibiotic treatment, special hygienic measures were taken for keepers, indoor enclosures and the central rock formation of the outdoor enclosure were thoroughly cleaned and the top layer of sand in the outdoor enclosure was turned over and mixed. About two weeks later another two weak and cachexic female baboons (one juvenile and one adult) were euthanised. When none of the weekly faeces samples of elephants and baboons tested positive for *Salmonella* for five weeks, it was concluded that the infection was over and baboons and elephants could use their mixed outdoor enclosure again.

Although the origin of infection remained unknown, it seemed most likely that the baboons were responsible for contaminating the elephants, because the baboons' preceding bronchitis probably weakened their immune system making them more susceptible to infection with *Salmonella* and because they showed the first symptoms of salmonellosis. It should be mentioned however that *Salmonella typhimurium* was isolated from the faeces of one elephant keeper as well, so transmission from the keeper to baboons and elephants cannot be excluded. Until now, no more outbreaks of salmonellosis occurred.

Interspecific interactions

Although competition over food is limited now, it still occurs occasionally. However, it has never resulted in accidents and both species can get enough food. Agonistic interactions outside food context occur infrequently. Sometimes the elephants chase all the baboons to the rocks, tease the baboons on the rocks with their trunk, throw small rocks or branches at the baboons (or the visitors) or splash them with water. This always results in panic among the baboons and makes them flee to the rocks where most females position themselves on the safe side of their males (i.e. the opposite side of the elephant). However, baboons always have the opportunity to move out of reach (e.g. on top of the rocks) or even out of sight (behind the rocks) of the elephants and the latter give up chasing or teasing the baboons with their trunk fairly rapidly. If a female or juvenile screams at a harassing elephant, adult males usually defend them by threatening or occasionally attacking, striking and even biting the elephant (which the males also do when they are fed up with the elephant themselves) (fig. 2). However, the latter ignores this most of the time and even a small movement is enough to make the male baboon flee again.

The most remarkable non-agonistic interspecific interaction is the riding of (mostly juvenile or subadult) baboons on the back of some elephants (fig. 3). This be-



Fig. 2: Hamadryas male threatening harassing elephants (photo: R. Deleu).

haviour was first observed at the end of the year baboons and elephants were introduced to each other, but it only became a regular interaction a few years later. The elephants actually invite baboons to climb on their back by putting their trunk on the rocks and staying there until a baboon jumps on its back (fig. 4). When baboons are on the elephants' back and the elephants are moving too much, the baboons quickly jump to the ground. On a few occasions juvenile baboons were seen jumping from one elephant's back to the other's. The baboons on the elephants' back rarely even seem to groom them shortly or else pick seeds, insects or parasites from their back.



Fig. 3: Juvenile baboon riding on the back of an elephant (photo: R. Deleu).



Fig. 4: Elephant inviting baboons to climb on his back by putting his trunk on the rocks (photo: R. Deleu).

Changes in behaviour associated with the mixing of species

Spatial use of enclosure

The elephants remain in the forested part of the enclosure most of the time, but four of them regularly go to the open part for bathing, foraging in the surrounding moat or interacting with the baboons. There is no evidence that the elephants would use the enclosure much differently if baboons were not present. For baboons the spatial use of the enclosure is largely influenced by the presence of elephants: most of the time the baboons avoid the elephants, so the latter determine where baboons are and the baboons have to be alert all the time. The central rock formation is a safe haven for baboons: they mainly use the rocks and immediate surroundings for resting and grooming and the other parts of the enclosure for travelling, foraging and drinking. As soon as the baboons feel threatened by an approaching elephant, they flee to the rocks (or to the other part of the enclosure) (fig. 5). In addition, baboons try to avoid places where there is an elephant between them and the rocks. When travelling in the proximity of elephants, the males usually position themselves between the elephants and their females. Overall cohesiveness of OMU's seems higher than in traditional single-species groups. The impact of the elephants' presence on the baboons' spatial use of the enclosure is supported by the observation that baboons spend more time resting and grooming during autumn and winter when some parts of the enclosure are inaccessible for the elephants.



Fig. 5: Baboons fleeing for an approaching elephant (photo: R. Deleu).

Time budgets

The mixed exhibit has a profound effect on activity levels of both species through frequent interspecific interactions, but for baboons time budgets are influenced even more indirectly. First, baboons forage several times a day in fresh or non-fresh elephant dung (fig. 6). In fresh dung, the baboons search for undigested food items (e.g. pieces of apple or carrot) and seeds. As soon as an elephant shows the first signs of defecation (spread hind legs and/or lift tail), alert baboons approach it in order to be the first to search through the dung and get the best bits (fig. 7). In non-fresh dung (that is spread out and from which most undigested items have disappeared), the ba-

boons probably search for insects. Furthermore, baboons forage several times a day in the leftovers of the elephants' hay. They only do this when the elephants are not in proximity (e.g. when elephants are fed or when elephants are in the open part of the enclosure). And finally, baboons occasionally forage (in search of seeds and insects) and, in case of juveniles, play in holes dug by the elephants.

With respect to time budgets it is also important to mention that little or none stereotypic behaviour can be observed in either species. One of the elephants sometimes performs stereotypic behaviour when the other elephants are in the open part of the enclosure she does not dare to enter: she then moves back and forward near the overflow of the basin until the others return (puts forelegs over the overflow and retreats them again). This behaviour probably is a result of stress from being separated from her herd, rather than from the presence of baboons.



Fig. 6: Adult male baboon foraging in fresh elephant dung (photo: R. Deleu).



Fig. 7: baboons approaching a defecating elephant and waiting for fresh dung (photo: R. Deleu).

Education and Scientific Research

From the previous paragraphs, it must be obvious that this mixed enclosure of baboons and elephants is more appealing to the public than traditional single-species enclosures. This is illustrated by seemingly longer periods visitors observe baboons and elephants in Safari Beekse Bergen than in traditional zoos. Therefore, the enclosure also provides more educational opportunities. Spread out over the three observation posts for visitors, different educational boards explain ecology and behaviour of both species. During holidays and weekends, (voluntary) guides are stationed near the mixed exhibit who can answer to the numerous questions of visitors on baboons, elephants and their interactions. In addition, an educational program has been developed for secondary schools to observe the baboons for determining time budgets, which is more feasible then elsewhere because of the raised activity levels.

Mixed exhibits are also more interesting for conducting ethological studies. Since 2000 the baboons are studied by the first author in the frame of a Ph.D. study on the flexibility of female social relationships in hamadryas baboons. The group was chosen next to a traditional single-species captive group (at Antwerp Zoo in Belgium)

and a wild group (in Kubkub, Eritrea), because the presence of elephants might mimic the presence of predators in their natural habitat: baboons have to be constantly alert and safe positions could be an important resource for competition. Some smaller behavioural studies were carried out on elephants and baboons in the beginning of the association as well.

Discussion

The mixed-species exhibit of hamadryas baboons and African elephants in Safari Beekse Bergen has proven to be successful. All cited advantages of mixed-species exhibits (CROTTY, 1981; HARDIE, S.M., 1997; THOMAS and MARUSKA, 1996) are present. First of all, no separate daytime enclosures are needed for the two species, which makes it possible to give both species a larger enclosure (and in the end reduces costs). Secondly, the mixing of species makes the environment more stimulating by increasing social complexity. Interspecific interactions result in increased activity levels and increased alertness (especially for baboons since they usually avoid the elephants). The presence of the other species also leads to the promotion of species-specific behaviours. Baboons use the enclosure as they would use their habitat in the wild: the central rock formation is a safe haven for resting and grooming while the rest of the enclosure is mainly used for foraging. Foraging in elephant dung can be observed in wild baboons as well (*Papio hamadryas cynocephalus*: P.C. LEE and J. PHILIPS-CONROY, pers. comm.). Elephants only digest about 44% of the food eaten and a lot of undigested food items and seeds are present in elephant dung (SHOSHANI, 1992). In addition, a lot of insects are attracted to the elephant dung, making it an excellent secondary food source for baboons. Although the possibility of agonistic encounters is one of the main criticisms on mixed-species exhibits (THOMAS and MARUSKA, 1996), it should be noted that agonistic encounters between species occur in the wild as well and could hence be seen as behavioural enrichment given frequencies are low. Wild African elephants were for example observed displacing baboons from waterholes (*Papio hamadryas cynocephalus*: D.R. RASMUSSEN, pers. comm.), throwing mud, soil and vegetation at a white rhino (WICKLER and SEIBT, 1997) and sand at a car (CHEVALIER-SKOLNIKOFF and LISKA, 1993). In addition young elephants were seen chasing baboons in the wild for no apparent reason, which has been interpreted as play (*Papio hamadryas anubis*: SHOSHANI and EISENBERG, 1992; *Papio hamadryas cynocephalus*: P.C. LEE, pers. comm.). Since the female elephants are relatively young, the occasional teasing of baboons can also be seen as play behaviour (although the baboons do not interpret it that way). Moreover, these agonistic interactions promote species-specific behaviour in baboons: the protective behaviour of hamadryas males against elephants can also be observed against predators in the wild (KUMMER, 1995; ZINNER and PELAEZ, 1999; ZINNER et al., 1999-2000). Furthermore, the mixing of baboons and elephants also resulted in the development of a special behaviour: baboons riding on the elephants' back. Baboons have been observed to ride on the back of ungulates in mixed exhibits of other zoos as well: hamadryas baboons on Nubian ibexes in Tierpark Hellabrunn in München, Germany and gelada baboons on barbary sheep in Wilhelma Zoologisch-Botanischer Garten in Stuttgart, Germany. And finally, the exhibit is more attractive for visitors and more interesting for education and scien-

tific research. The combination of elephants and baboons also provides an excellent opportunity to make people aware of animal-human conflicts and the consequences for conservation, since both species are notorious for crop raiding (baboons during daytime and elephants at night) and are often chased and killed by local farmers (baboons: HILL, 2000; ZINNER et al., 1999-2000; African elephants: HOARE, 2000). It could be argued that the species for this aggregation are not very well chosen for educational purposes, because it is not sure if hamadryas baboons and African elephants still live sympatrically today. However they have lived sympatrically in Eritrea, Ethiopia and Somalia (probably until the middle of the last century) and there is a chance that they still do in the Babile Elephant Sanctuary south of Harar in Ethiopia (YALDEN et al., 1977, 1986). In addition, other baboons still live sympatrically with African elephants today.

Disadvantages of this mixed-species exhibit on the other hand are very limited. First, agonistic encounters are relatively infrequent and have never resulted in injuries or detrimental levels of stress. Stereotypic behaviour is almost absent in both species and reproduction in baboons was not influenced negatively on the long term. In fact the majority of females had to be sterilised to prevent the group from growing too fast. Infant-mortality (probably as a consequence of infanticide) was extremely high in the beginning of the association, which suggests that stress associated with the introduction of the elephants might have been the cause although it might have been related to the relocation as well. Although infanticide remains a problem in this group, there is no evidence that it is associated with the presence of elephants. Most dead infants are first noticed when baboons are released in their outdoor enclosure in the morning, suggesting that inferred infanticides occurred at night. In addition, zoological records of the former Windsor Safaripark showed that infanticide occurred in this group before and that infant mortality was high before as well. Furthermore, infanticide is also observed frequently in captive hamadryas baboons in single-species exhibits (RIJKSEN, 1981; ZINNER et al., 1993; LEINFELDER, 2001). The plans to start reproduction in elephants will be an important test case for the mixed exhibit, since baboons might harass young elephants. Subadult male baboons have been observed to attack and chase a young elephant in the wild (*Papio hamadryas anubis*: R.M. SAPOLSKY, pers. comm.). It should further be noted that fur-condition of some baboons is poor (a lot of bald patches and some males almost completely lack a mantle). There is no evidence however that this is a consequence of the presence of elephants, but rather seems to be related to periodical fighting over females between the males. Secondly, the incident with the *Salmonella* infection of baboons and elephants demonstrates that cross-contamination can be a problem. Because *Salmonella* infections are common in captive primates (MARTIN, 1978) and salmonellosis is often fatal in elephants (SCHMIDT, 1978), this problem seems serious since baboons might increase the risk of infection in elephants through zoonosis in a mixed exhibit. It is impossible to prevent the baboons from killing and eating free living water birds like ducks, swans and gulls that dwell in the surrounding moat or the quagmires and are known as carriers of *Salmonella* (STEELE and GALTON, 1971). However, salmonellosis has been reported frequently in captive elephants in single-species exhibits and the source of infection can be contaminated food, water or people as well (SCHMIDT, 1978; MELTZER, 1993). The fact that no elephant died from salmonellosis in this group is probably related to the baboons

serving as "indicators": isolation of the *Salmonella* bacteria from the euthanised baboons made it possible to make an antibiogram so non-resistant antibiotic treatment could be started in time (HUBER and KAANDORP, in press). It thus can be concluded that the potential raised threat of salmonellosis in elephants through association with baboons is not an insuperable problem as long as health of both species is closely monitored.

Possible factors that could be responsible for the success of this mixed-species exhibit are the following (THOMAS and MARUSKA, 1996). First, the enclosure was new to both species so exploration of the area diverted the animals' attention from the other species after the introduction. Secondly, animals occupy similar niches and have similar lifestyles but are of markedly different size so aggressive competition can be averted. Furthermore, competition over food is limited because baboons and elephants are fed separately and because there is enough of the elephants' hay left for the baboons. Thirdly, the enclosure is large so baboons can easily avoid the elephants as they do most of the time in the wild as well (*Papio hamadryas cynocephalus*: P.C. LEE and *Papio hamadryas anubis*: R.M. SAPOLSKY, pers. comm.). The central rock formation can function as a visual barrier and safe haven for baboons (in addition to the parts of the enclosure inaccessible for elephants). Since elephants can successfully chase baboons away if necessary, there is no need for an area that elephants can use undisturbed. And finally, the baboons had been kept in a mixed-species exhibit before, so they were used to interacting with other species.

In conclusion, the mixed exhibit of African elephants and hamadryas baboons existing for eight years now, has been a tremendous success. No accidents have happened and baboons and elephants interact frequently, making the mixed exhibit an excellent, cheap and educational way of behavioural and environmental enrichment.

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Authors' addresses:

Deleu, R., Nelissen, M.: University of Antwerp, Behavioural Biology, Groenenborgerlaan 171, B-2020 Antwerp, Belgium. E-mail: rebekka.deleu@ua.ac.be
Veenhuizen, R.: Safari Beekse Bergen, Beekse Bergen 31, 5081 NJ Hilvarenbeek, the Netherlands. E-mail: Veenhuizen27@zonnet.nl

TEN YEARS OF TAMARIN MIXED-SPECIES TROOPS AT BELFAST ZOOLOGICAL GARDENS. HARDIE, S.M., PRESCOTT, M.J. AND BUCHANAN-SMITH, H.M.

Key words: *Callimico goeldii*, captivity, free-ranging, *Saguinus fuscicollis*, *Saguinus labiatus*

Abstract

In the wild, tamarin species form some of the longest lasting and most cohesive of primate mixed-species associations. Despite this, they are usually exhibited in captivity as single-species troops. Here we describe and integrate both published and unpublished research conducted at Belfast Zoological Gardens, Northern Ireland, concerning the formation and maintenance of mixed-species troops of the saddle-backed tamarin (*Saguinus fuscicollis*) and the red-bellied or white-lipped tamarin (*Saguinus labiatus*). Over a 10-year period, a protocol for successful mixing was established, and at least 26 mixed-species troops were formed and maintained off-exhibit to the public with few or no problems; some individual animals lived in such troops for over 3.5 years. Detailed research comparing single- and mixed-species troops of tamarins demonstrates that both species actively attend to and respond to each other in mixed-species troops, and that they alter their behaviour in ways that are complementary and potentially beneficial. Both tamarin species successfully bred and reared offspring whilst in mixed-species troops. Free-ranging mixed-species troops showed a high degree of cohesion, demonstrating that such troops in captivity are not based simply on the species tolerating each other's presence in a confined space. An informative exhibit of a tri-specific troop of both the saddle-backed and red-bellied tamarin with Goeldi's monkey (*Callimico goeldii*), another species with whom the tamarins associate in nature, was opened to the public in 1997.

Introduction

Primate mixed-species troops in captivity

The traditional way of exhibiting primates in captivity has been to house them as single-species troops. That said, there have been attempts at housing different species of primates together, as well as with non-primates. Mixing has involved most of the major primate taxa, ranging from orang-utans (*Pongo*) with gibbons (*Hylobates*), gorillas (*Gorilla*) with colobus monkeys (*Colobus*), to howler monkeys (*Alouatta*) with spider monkeys (*Ateles*) (BAKER, 1992). The success of these groupings has been quite varied (e.g. XANTEN, 1992; THOMAS and MARUSKA, 1996).

From a number of different perspectives it would appear beneficial to house captive primates in mixed-species troops. In terms of benefits to the individual animals themselves, mixed-species troops have been shown to lead to an increase in activity (e.g. HEYMANN et al., 1996; HARDIE, 1997) and this, combined with increased social complexity and stimulation may correspond to an increase in psychological

wellbeing. Another potential benefit includes increased space, for example, by combining access to pre-existing enclosures (BAKER, 1992; CHAMOVE, 1989; XANTEN, 1990, 1992).

If the animals are part of a captive breeding programme for conservation, then it is vital that they interact within, and learn about, a social environment that is as natural as possible (e.g. BECK, 1991; POOLE, 1991). Displaying animals in an appropriate social context also has the associated benefit of being more educational for the public. It allows visitors to observe inter-specific interactions and learn about mixed-species associations, which in turn presumably makes for a more interesting and enjoyable zoo experience (BUCHANAN-SMITH et al., 2001; XANTEN, 1992).

Regardless of these advantages, forming and maintaining mixed-species troops is not straightforward or risk-free. SODARO (1999) highlights the fact that short-term success may ultimately lead to long-term failure and that such troops may require a greater level of monitoring than each species requires when on its own. Problems sometimes do not present themselves instantly (THOMAS and MARUSKA, 1996). For example, particular attention needs to be taken around the time of births because inter-specific aggression may increase (BUCHANAN-SMITH, 1998). Temporary separation of the species is one management solution for dealing with such problems (BAKER, 1992; HARDIE, 1997).

Callitrichid mixed-species troops in captivity

There have been numerous attempts in a variety of different zoos to form mixed-species troops with members of the taxonomic family Callitrichidae (consisting of lion tamarins, *Leontopithecus*; tamarins, *Saguinus*; marmosets, *Callithrix*; pygmy marmosets, *Cebuella*; and Goeldi's monkey, *Callimico*) but the results have been somewhat mixed (see SODARO, 1999 for a review). Successful pairings include common marmosets (*Callithrix jacchus*) with black-handed spider monkeys (*Ateles geoffroyi*), dusky titi monkeys (*Callicebus moloch*) with golden lion tamarins (*Leontopithecus rosalia*), and golden lion tamarins with Geoffroy's tufted-eared marmosets (*Callithrix geoffroyi*), as well as mixing callitrichids with non-primate species (SODARO, 1999; XANTEN, 1990). Unsuccessful pairings include the dusky titi monkeys with several callitrichid species, including silvery marmosets (*Callithrix argentata*), Goeldi's monkey and pygmy marmosets (*Cebuella pygmaea*). In terms of mixing callitrichids together, SODARO (1999) reported that 16 species have been tried in mixed-species combinations at more than 20 different AZA accredited institutions. He reports more than 50 separate attempts to form mixed-species exhibits, and the success rate was somewhere around 66 %. Success included mixing emperor tamarins (*Saguinus imperator*) with pygmy marmosets, and red-bellied tamarins (*Saguinus labiatus*) with pygmy marmosets. These species are sympatric in nature.

One key aspect related to the success of any mixed-species exhibit seems to be the species chosen (THOMAS and MARUSKA, 1996). However, XANTEN (1992) commented upon successful attempts and emphasised that he considered the main factor to be the behaviour of individuals rather than species-specific tendencies. The research we describe below from Belfast Zoological Gardens on tamarin mixed-species troops suggest that both these factors are important, but that one of the main considerations for successful mixed-species troop formation is that the species are both sympatric and form associations in the wild (HARDIE et al., 1993).

Tamarin mixed-species troops in the wild

Tamarins are small, arboreal insectivore-frugivores, weighing from 320 to 560g, living in troops of around five to ten individuals (RYLANDS et al., 1993; HEYMAN and BUCHANAN-SMITH, 2000). There are currently 15 species recognised, with a total of 33 subspecies (RYLANDS et al., 2000), distributed throughout the entire northern and western Amazon. The saddle-backed tamarin (*Saguinus fuscicollis*) has the largest distribution of the tamarins, and in areas where its geographic distribution overlaps with members of HERSHKOVITZ'S (1977) *mystax*-species group (*S. mystax*, *S. labiatus*, *S. imperator*) they form mixed-species troops (e.g. TERBORGH, 1983; HEYMANN and BUCHANAN-SMITH, 2000). Throughout this range of overlap, these species are normally found in association.

Within such troops, species show divergence in factors such as body size, vertical stratification and insect foraging strategy (e.g. HEYMANN, 1997; HARDIE, 1998; BUCHANAN-SMITH, 1990, 1999a; HEYMANN and BUCHANAN-SMITH, 2000). For example, saddle-backed tamarins usually occupy a lower part of the forest than their congener (associating tamarin species) and travel more by means of vertical clinging and leaping between vertically orientated substrates. Such divergence likely permits their association. Interactions between the species are rare, and this applies to both agonistic and affiliative events (TERBORGH, 1983; HEYMANN and BUCHANAN-SMITH, 2000). During agonistic events, saddle-backed tamarins appear to be dominated by their congeners (e.g. TERBORGH, 1983; PERES, 1991; Porter, 2001a). Such encounters most often occur in small feeding trees (HEYMAN, 1990) where high dietary overlap for plant food sources may bring the species into direct competition (HEYMAN and BUCHANAN-SMITH, 2000; PORTER, 2001a). However, agonism rarely involves physical contact and usually occurs in the form of displacement of the subordinate individual from the preferred location (HEYMAN and BUCHANAN-SMITH, 2000).

Mixed-species tamarin troops are remarkably long-lasting and cohesive (HEYMAN and BUCHANAN-SMITH, 2000). The troop shares a common territory and defends it from neighbouring mixed-species troops; individuals are only aggressive to members of their own species (e.g. TERBORGH, 1983; BUCHANAN-SMITH, 1990, 1991). Mixed-species troops are also highly co-ordinated in terms spatial distribution; associating species typically being found within 20-50 m of each other for a large percentage of their time (often exceeding 80 % of their daily activity) (TERBORGH, 1983; HEYMANN and BUCHANAN-SMITH, 2000). The stability and active nature of their associations, the high degree of spatial cohesion and the fact that relatively little inter-specific aggression is observed, makes tamarins ideal candidates for forming mixed-species troops in captivity.

The present study concentrates on the association between Weddell's saddle-backed tamarin (*S. fuscicollis weddelli*) and the red-bellied or white-lipped tamarin (*S. l. labiatus*). Mixed-species troops of these species have been the subject of several field studies in northern Bolivia (e.g. POOK and POOK, 1982; BUCHANAN-SMITH, 1990, 1999a; HARDIE, 1998; PORTER, 2001a,b), where these species have also been shown to form mixed-species troops with Goeldi's monkeys. PORTER (2001a,b) reports that Goeldi's monkeys may be found in contact with tamarins for anything up to 89 % of their daily activity period. However, unlike the association between tamarin species, Goeldi's monkey does not associate with only one tamarin

mixed-species troop, but instead has a much larger home range which may encapsulate at least six separate tamarin troops (PORTER, 2001b). Goeldi's monkey is usually found at a lower forest stratum than both saddle-backed and red-bellied tamarins, and has lower dietary overlap with the tamarins compared to that between the tamarin species themselves (CHRISTEN and GEISSMANN, 1994; PORTER 2001a). Like the tamarin species, Goeldi's monkey does not have many interactions (neither affiliative nor agonistic) with its associating species (PORTER, 2001a). The natural association between Goeldi's monkeys and tamarin species in the wild makes them realistic candidates for forming tri-specific mixed-species troops in captivity.

Tamarin mixed-species troops in captivity

Prior to the start of the research at Belfast Zoological Gardens (Belfast Zoo), there was only one detailed report of a captive tamarin mixed-species troop. It consisted of wild-caught Spix's moustached tamarins (*S. m. mystax*) and Geoffroy's saddle-backed tamarins (*S. fuscicollis nigrifrons*). The troop was held at Iquitos, Peru, in a cage measuring 9 x 13 x 2.5 m and over a period of over 5 years troop sizes ranged as high as nine saddle-backed and seven moustached tamarins (HEYMANN and SICCHAR, 1988). Both species bred in the enclosure, with eight saddle-backed and five moustached infants being successfully reared in the mixed-species troop.

We concluded from Heymann and Sicchar's study, that it is possible to keep tamarins in mixed-species troops in captivity. However, as this mixed-species troop was made up of individuals that were wild-caught, and since no details were given of the method used to form the troop, it was not clear whether mixed-species troops of tamarins could be formed from animals born in captivity and reared as single-species groups. An examination of the concept of forming and maintaining tamarin mixed-species troops formed the basis of much of our early research on captive mixed-species troops at Belfast Zoo.

An historical review of tamarin mixed-species troops at Belfast Zoo

This section describes the development of the tamarin mixed-species troop research project at Belfast Zoo over the 10 years between 1992 and 2002 (see HARDIE et al., 1993; HARDIE, 1997; BUCHANAN-SMITH et al., 2001). In the early 1990s Belfast Zoo was one of the few European zoos that had a collection of Weddell's saddle-backed tamarins and although they initially did not hold the sympatric and associating red-bellied tamarin they had past experience of this species and were willing to obtain some animals for the project. In addition, Belfast Zoo had been extensively redeveloped over a period of time (BUCHANAN-SMITH et al., 2001) and had suitable off-exhibit area which they were willing to give over to the research project (HARDIE, 1997). It should be noted that the studies described below were not done specifically to examine the stability of mixed-species troops, and indeed experimental protocol required the separation of mixed-species troops for research purposes, despite peaceful cohabitation.

Phase 1: July 1992 to September 1997

The initial start-up of the project involved acquisition of red-bellied tamarins from other zoo collections, construction of suitable enclosures, and establishing a

protocol for successfully combining single-species groups into mixed-species troops. The protocol which was developed, and a preliminary evaluation of the success of this approach to exhibiting tamarin species, is outlined in a publication covering the first 4 years of research (HARDIE, 1997). Specifically, HARDIE (1997) describes 11 attempts to form mixed-species troops (all consisting of at least one male-female pairing of each species, Table 1) and reports that this is a satisfactory method of exhibition for the animals involved. One of the unsuccessful mixings consisted of an old male saddle-backed tamarin attacking the red-bellied tamarins, while the other involved the female red-bellied tamarin attacking the saddle-backed tamarins. This suggests that individual personalities can play a key part in whether the troop is stable.

Table 1: Summary of mixed-species troop formation (HARDIE 1995, PRESCOTT 1999).

Time period and reference	Number of pairing attempts	Success	Largest number of separate pairings
1992-1996 (HARDIE, 1995, 1997)	11	82 % (9/11)	1 red-bellied group with 2 different groups of saddle-backed tamarins
1996-1997 (PRESCOTT, 1999)	15	100 % (15/15)	1 saddle-backed group with 3 different groups of red-bellied tamarins
Total/mean %	26	92.3 %	

Subsequent to these experiments, Prescott carried out further experimental work with some of the same troops and other additional troops. In terms of HARDIE'S (1997) original mixed-species troops, PRESCOTT (1999) maintained four of these, with only occasional temporary separation for experimental reasons. Individuals in these troops were thus part of the same mixed-species troop for over 3.5 years with no problems (Table 1). In total, Prescott maintained 15 different pairings of species, including six mixed-species troops that were made up of individuals entirely different from those used by HARDIE (1995, 1997). One group of saddle-backed tamarins was paired with three separate groups of red-bellied tamarins, demonstrating the flexibility of the pairings.

Summary of experimental findings and their implications for mixed-species troops

Once the mixing-protocol was established, we undertook a series of experiments to elucidate the advantages and disadvantages of mixed-species troop formation to individuals of each species. This research centred on a paradigm that involved the systematic comparison of single- and mixed-species troops (see BUCHANAN-SMITH and HARDIE, 1997 for details), to test hypotheses as to why tamarins form associations in the wild. The two major classes of hypotheses we tested were the decreased predation hypothesis and the foraging benefits hypothesis (see HEYMANN and BUCHANAN-SMITH, 2000 for a review).

Our early studies examining species differences, and comparing the behaviour of single- and mixed-species troops found significant differences in their behaviour. In mixed-species troops, the tamarins conformed to the pattern seen in the wild; most of our captive studies showed that the two species segregated themselves by height (with red-bellied tamarins higher than saddle-backed tamarins), and diverged in preferred substrate use (both size and orientation) and locomotion, in a way that was broadly similar to the pattern found in wild tamarins (HARDIE, 1995; and see HEYMANN and BUCHANAN-SMITH, 2000 for a review). Few inter-specific social interactions were observed; those that were observed were primarily of red-bellied tamarins displacing saddle-backed tamarins from preferred food or locations (e.g. HARDIE, 1995). Inter-specific grooming was very rare (5 events in 128 hours of observation: HARDIE, 1995), but the tamarins would sometimes sleep together in the same nest box despite more than one box being available (HMBS, pers. obs.).

In terms of changes in behaviour, we found that the tamarins engaged in more foraging in mixed-species troops than in single-species groups (BUCHANAN-SMITH, 1999b) whilst less time was spent being vigilant (HARDIE and BUCHANAN-SMITH, 1997). This demonstrates that individuals of both species alter their behaviour in response to the presence of the other species. However, the same decrease in individual vigilance applies to forming larger single-species groups (e.g. CAINE, 1986) and therefore this advantage is not specific to mixed-species troops per se, but simply a consequence of increased group size. Further analyses of the vigilance data shows that although the overall vigilance rates of the two species do not differ, red-bellied tamarins look upwards significantly more than saddle-backed tamarins in both single-species groups and mixed-species troops. However, the saddle-backed tamarins take advantage of the upward scanning of the red-bellied tamarins as they perform significantly less looking up in mixed-species groups than in single-species troops, whereas the rate of looking up is not significantly different for the red-bellied tamarins (BUCHANAN-SMITH and HARDIE, 1997). Therefore the behaviour is not simply a consequence of increased group size, but specific to the presence of a different species, with different behavioural propensities.

Our studies have also demonstrated that the two tamarin species learn as well from conspecifics (members of the same species) as they do from heterospecifics (members of a different species). We have shown that they can learn from both conspecifics and heterospecifics about the location of food, the quantity and palatability of food and how to access food in a novel task (HARDIE, 1995; PRESCOTT, 1999; PRESCOTT and BUCHANAN-SMITH, 1999, 2002, in prep). Taken together these studies suggest that the tamarins in mixed-species groups are not avoiding each other or simply tolerating each other's presence, but actively attending to, and responding to, the other species in potentially beneficial ways, similar to those observed in the wild (see HEYMANN and BUCHANAN-SMITH, 2000 for a review).

Phase 2: Free-ranging troops established from 1993 onwards

In the mid-1980s an innovative approach was taken towards the exhibition and husbandry of captive golden-lion tamarins (*L. rosalia*) at the National Zoological

Park, Washington. This involved allowing a family of six tamarins to roam freely in a quiet area of the zoo (BRONIKOWSKI et al., 1989). The approach was successful and has since been applied to lemurs at Belfast Zoo (*Lemur catta* and *Eulemur macaco*: SMH pers. obs.) as well as to cotton-top tamarins (*S. oedipus*) at Jersey Wildlife Preservation Trust (e.g. PRICE et al., 1989, 1991) and at Edinburgh Zoo (MJP & HMB-S pers. obs.). The goal of free-ranging exhibits has often been to allow animals to adapt to more natural surroundings than those usually used in zoos (BRONIKOWSKI et al., 1989) and this can be a first step towards the "training" of captive-born tamarins in preparation for reintroduction into the wild (e.g. golden-lion tamarins, BECK et al., 1990). Free-ranging animals benefit over their truly captive counterparts gaining a greater degree of freedom while still being provisioned and monitored for health. In addition to the potential for improved welfare that the greater space, environmental complexity and unpredictability that free-ranging may afford the primates, free-ranging exhibits primates are attractive and potentially more informative for the public. The primates have the opportunity to engage in more species-typical behaviour, for example locomotion and foraging, in a more naturalistic environment.

Free-ranging mixed-species exhibits also have important implications for our understanding of both captive and wild mixed-species troops. Despite the fact that mixed-species tamarin troops can be formed in captivity (HARDIE et al., 1993; HARDIE, 1997; HEYMANN et al., 1996), there is a validity question in terms of whether or not these situations are essentially the same. How do you decide whether two species in a confined space are associating or simply tolerating one another in forced proximity? Although different researchers have used different definitions for association, there is general agreement that association can be defined as a coincidence in time and space that is not due to chance encounters alone (see WASER, 1980, 1984). In a conventional captive situation, by necessity, the species have to share an area that is very small in size when compared to their natural range size. Individuals cannot avoid each other even if they want to.

This is where the free-ranging exhibit comes into play. As the two species need not be constrained within a limited area, it can be concluded that any relationship that occurs will be through some level of "choice" (as each has the potential space available to avoid each other) and not forced, as in the enclosed areas. If the species show some sort of cohesion, whereby both are close temporally and spatially, then one can conclude that these species really do actively choose to associate in captivity. On the other hand, if the species do not associate in any clear and coherent way, it may suggest that the association is not the same as in wild tamarins, and suggests that captive mixed-species troops are not forming associations, but are merely tolerating each other's presence in a confined area. This is extremely important, as if the two species are not shown to associate then it is difficult to provide justification for forming mixed-species troops in captivity as it may actually be detrimental to their welfare. The purpose of studying the free-ranging tamarin troops was therefore to determine whether the two species would show a greater than chance coincidence in time and space, i.e. they should spend time close to each other, and not avoid each other. Here we report the findings relating to this from two unpublished theses (HARDIE, 1995; MCSHANE, 1995).

Study animals and release procedure

Two mixed-species troops were released on separate occasions into the same wooded area within the zoo grounds, but off-exhibit to the public. Each troop consisted of an adult male-female pair of each species. The troops were initially held for four weeks in a small, purpose built cage (4.6 x 3.1 x 2.5 m), which had two centrally placed heated and insulated boxes raised from the ground. The enclosure was built around a tree, whose branches connected the enclosure with wooded area where the troop was expected to free-range. The monkeys could potentially range within the zoo grounds for distances up to 60 m. Prior to the release, a detailed map of the free-range area was constructed, and divided into 2 x 2 m quadrats to allow quantification of the tamarins' position (Figure 1).

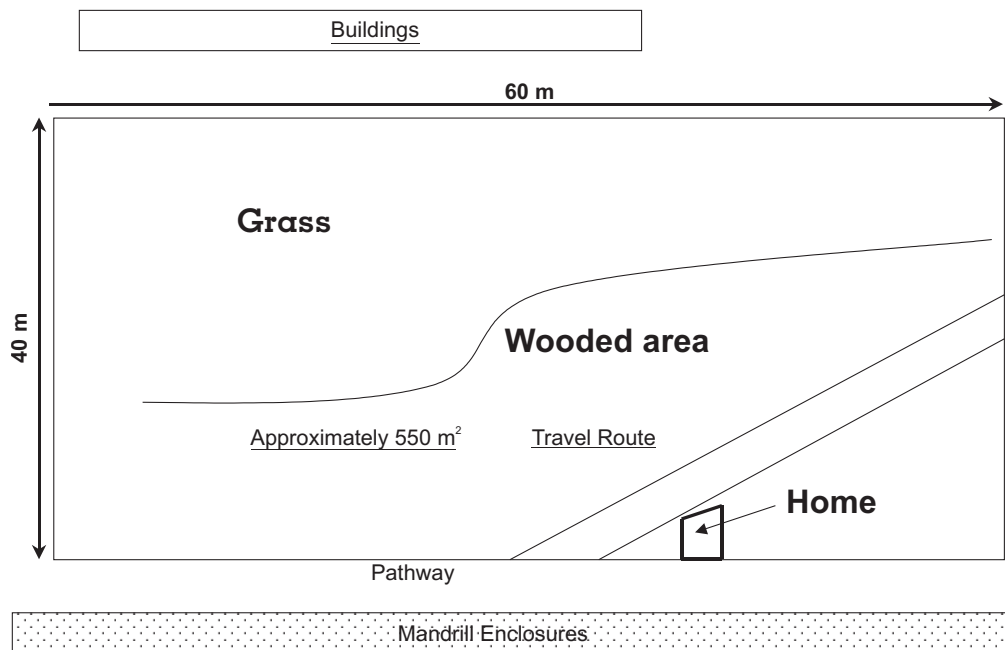


Fig. 1: Schematic map of free-ranging area at Belfast (not shown to scale).

Methods

The monkeys were fed at 0930 h, before any observations took place. Focal animal sampling was employed, and observations counterbalanced across morning and afternoon. Focal animal data were collected on nearest conspecific and heterospecific neighbour using instantaneous sampling (MARTIN and BATESON, 1993) with an interval of one minute. In addition, quadrat location was noted every two minutes. HARDIE (1995) collected a total of 128 hours of data, giving 32 hours for each focal, whilst MCSHANE (1995) collected a total of 38 hours (9.5hrs/focal), using an identical protocol.

Results: Measures of association

1) Range use

Hardie found that both species used 134 different quadrats (2 x 2 m); 53% of these were used by both species (Figure 2). Although the saddle-backed tamarins used 35 more quadrats than the red-bellied tamarins, suggesting that they are the more explorative of the two species, both species only spent 13.8 % of sample points in exclusively used quadrats. This means that approximately 86 % of all quadrat observations were when the species were in quadrats that they both used. This suggests that they did not avoid each other.

McShane also found a considerable overlap, and demonstrated that a total of 87 quadrats were used, with 47.73 % being used by both species. In this case, both species individually used an almost identical number of quadrats and they spent 26.1 % of observations in exclusively used quadrats. This meant that for 73.9 % of the time they were found in the shared area of the space, and confirms HARDIE'S (1995) finding that the tamarins did not avoid each other.

2) Nearest neighbour distances

Most mathematical formulations of association usually involve the interpretation of distances between individual troop members, both within and between species (WASER, 1982, 1984, 1987). However, the formulae invariably use some measure of population density and so were clearly inappropriate in the present captive study. On the other hand it is possible to compare the average within species and between species spacing. This gives an indication of how close the subjects are generally to conspecifics, compared to how close they are to heterospecifics. HARDIE (1995) and MCSHANE (1995) found that the mean nearest conspecific distance was 1.8 and 3.0 m for red-bellied tamarins and 2.7 and 2.4 m for saddle-backed tamarins respectively. The mean distance to the nearest heterospecific was 4.5 and 5.7 m (HARDIE, 1995; MCSHANE, 1995 respectively). This is only approximately twice the within group distance and indicates close coordination (Table 2). More impressive is the fact that both Hardie and McShane found that species were found within 10 m of each other for nearly 89 % of all observations, and about 63 % of observations they were 5 m or less from each other (Table 3). Given that the monkeys had a potential to be well over 10 m away from each other (up to over 50 m) this suggests an active association between them.

Table 2: Mean distance to nearest neighbour in two free-ranging mixed-species troops of tamarins.

	Red-bellied	Saddle-backed	Mean	Reference
Nearest conspecific	1.8 m 3.0 m	2.7 m 2.4 m	2.3 m 2.7 m	HARDIE, 1995 MCSHANE, 1995
Mean	2.4 m	2.6 m	2.5 m	
Nearest heterospecific	4.8 m 5.8 m	4.3 m 5.6 m	4.5 m 5.7 m	HARDIE, 1995 MCSHANE, 1995
Mean	5.3 m	5.0 m	5.1 m	

Fig. 2: Range overlap and quadrat use in two species of free-ranging tamarins. Values are based on position of focal individual at 2-minute sample intervals.

	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD			
19																															19	
18	<i>S. labiatus</i> only								X																						18	
17	<i>S. fuscicollis</i> only								*																							17
16	Range overlap																															16
15	Not recorded																															15
14	2 x 2 m Quadrat																															14
13																					X			*			X	X			13	
12															*	*			*						X		X	X			12	
11														X				*	*					X	X						11	
10							*				*	*	X																	*	10	
9			*	*					X													*		*	*	*	*	*	*	*	9	
8										X	X													*	*	*	*	*	*	*	8	
7				*		*	*	*	*															*	*	*	*	*	*	*	7	
6				*				*	*										*							*	*	*	*	6		
5			*					*	*					X										*	*	*	*	*	*	5		
4				*					*							*	*	*							*	*	*	*	*	4		
3									*					*		*	*	*													3	
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1																															1	
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	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD			

Table 3: Percentage of time the two species of tamarins spent within proximity to each other whilst free-ranging.

	< 50 cm	< 1 m	< 5 m	< 10 m	Total n	Reference
% observations within distance to conspecific	39.2 % 28.2 %	60.0 % 41.2 %	85.1 % 75.8 %	97.9 % 92.8 %	7680 2220	HARDIE, 1995 MCSHANE, 1995
Mean	67.4 %	50.6 %	80.5 %	95.4 %		
% observations within distance to heterospecific	5.4 % 4.6 %	40.4 % 21.4 %	64.7 % 60.6 %	89.4 % 87.9 %	7680 2220	HARDIE, 1995 MCSHANE, 1995
Mean	5.0 %	30.9 %	62.7 %	88.7 %		

Results: Interactions

Table 4 shows the interactions between the species that HARDIE (1995) recorded post-release. Interactions were observed at a rate of approximately 1.4 per hour of observation. Displacements and aggression were the most common forms of interaction, followed by huddling and vocalising. Concentrating on the direct interactions (excluding vocalising) these can be divided into agonistic (i.e. displacement & aggression – 54 % of interactions) and friendly (i.e. huddle, play, groom, solicitation & copulation – 29 %). The red-bellied tamarins were responsible for most agonistic encounters, initiating 87.6 % of all such interactions. They were also responsible for initiating 70.4 % of all friendly acts. The saddle-backed directed most vocalisations towards the red-bellied tamarins, often as a consequence of being displaced from preferred locations. One interesting interaction was of an inter-specific mating. The female red-bellied tamarin solicited the male saddle-backed tamarin to mate with her. He mated with her once, and was never observed mating with her again. His own mate was past breeding-age and resisted any sexual solicitation and attempted copulations by her partner (DAY, pers. comm.). The female red-bellied tamarin later gave birth to two stillborn infants who were clearly red-bellied offspring and the timing of birth suggested that the inter-specific mating occurred when she was already pregnant.

Table 4: Inter-specific interactions between members of a free-ranging mixed-species tamarin troop, at Belfast Zoo (HARDIE 1995, MCSHANE, 1995).

Behaviour	Red-bellied	Saddle-backed	Total n	Percentage
HARDIE, 1995				
Displacement	52	1	53	29.6 %
Aggression	33	11	44	24.6 %
Huddle	25	7	32	17.8 %
Vocalise	3	26	29	16.2 %
Play	8	5	13	7.3 %
Groom	3	2	5	2.8 %
Solicitation	1	0	1	0.6 %

Behaviour	Red-bellied	Saddle-backed	Total n	Percentage
HARDIE, 1995				
Copulation	0	1	1	0.6 %
Tongue flick	0	1	1	0.6 %
Total	125	54	179	
MCSHANE, 1995				
Displacement	8	6	14	40,0 %
Aggression	8	12	20	57.2 %
Tongue flick	1	0	1	2.8 %
Total	17	18	35	

MCSHANE (1995) found fewer interactions within her troop (< 1 per hr of observation) and no clear sign of any friendly interactions. She found that the saddle-backed tamarins showed marginally more aggression (18 vs. 17 acts), and stressed that this may have been due to the recent arrival of them into the area previously occupied by the red-bellied tamarins. It should be noted that although the red-bellied tamarins were displaced by their congeners on six occasions, they themselves displaced the saddle-backed tamarins eight times. Therefore, the dynamics within this troop were broadly similar to those in the other groups, and MCSHANE (1995) argues that aggression declined over the course of her study.

Phase 3: New enclosure built in 1996

In 1996, an enclosure on exhibit to the public was purpose-built for the display of a mixed-species troop (Figure 3) that initially consisted of 11 animals; one group consisting of a family of six red-bellied tamarins, and one group consisting of a family of five saddle-backed tamarins. Later, this enclosure was home to a tri-specific troop, of the two tamarin species together with a group of Goeldi's monkeys. This large enclosure measures approximately 12.6 x 12.4 x 6,0 m (at its highest point) and contains several large trees (5+ m tall) and shrubs. Two huts are situated around 4 m from the front of the enclosure, placed on a raised platform, approximately 1.5 x 1.55 m. Access inside these is via a hatch (0.3 x 0.3 m) covered with 5 cm wide overlapping polythene drapes. This hatch leads into an inside area of approximately 0.6 x 1.1 x 1,0 m. There is a divider separating the inside area into two; each side contains a nest box.

All three species have bred in this enclosure. However, despite the large size of the whole enclosure, the heated inside huts were not large, and particularly in cold weather, the species would be forced into close proximity with each other. Some animals, particularly the Goeldi's monkey, appeared intimidated and unwilling to enter the smaller huts, even in cold weather. It was necessary to remove all the animals from the exhibit in the winter for this reason (CHALLIS, pers. comm.). Larger heated indoor accommodation was built in 2001 (consisting of two rooms, each approximately 1.5 x 1.5 x 2.1 m) to counteract this problem. The frequency of agonism has decreased and the tri-specific troop can remain on exhibit throughout the year (CHALLIS, pers. comm.). This situation highlights an important point for the captive care of tamarin mixed-species troops; any resource, such as food, water, heated areas, or resting and sleeping sites, should be provided in multiple locations and the

animals should not be forced into close proximity which may detrimental to their welfare (e.g. see BUCHANAN-SMITH, 1998).

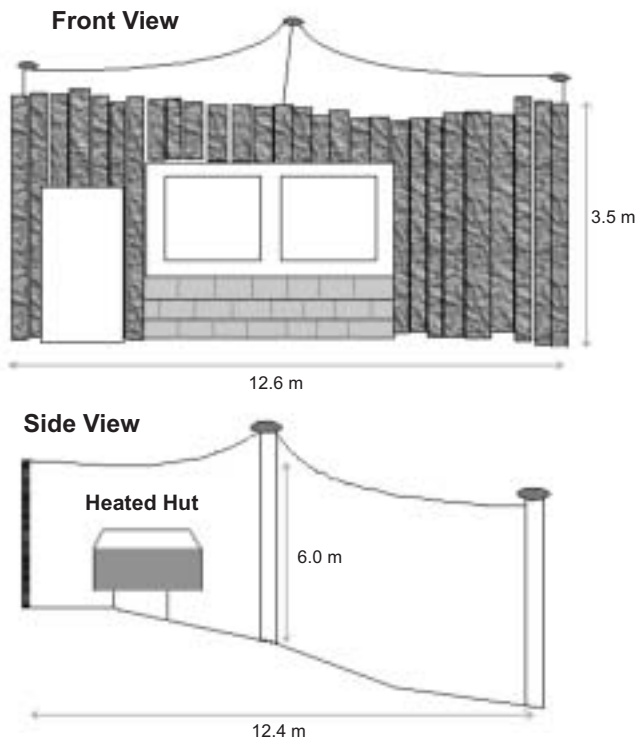


Fig. 3: New enclosure for tri-specific mixed-species troop, showing side and front views (not shown to scale).

Discussion

We have already published our findings that mixed-species troops of red-bellied tamarins and saddle-backed tamarins can be formed in captivity (HARDIE et al., 1993; HARDIE, 1997), and that many aspects of their behaviour show remarkable similarity to those of their wild counterparts (e.g. BUCHANAN-SMITH and HARDIE, 1997; PRESCOTT and BUCHANAN-SMITH, 1999). However, it was not clear whether these "associations" differed from mere mutual toleration in an enclosed area, or whether there was an active association between the species. The data we have presented here, suggest that both species actively attend to, and respond to the other species in potentially beneficial ways. Furthermore, they choose to stay in close proximity even when they can avoid each other. However, it may be that the association is more active on the part of one species. In the wild it is generally found that saddle-backed tamarins follow the red-bellied tamarins (e.g. BUCHANAN-SMITH, 1990). Future research may focus on whether both species of tamarins actively chose to associate with each other in captivity, as this clearly has implications for their well-being.

Tamarins in mixed-species troops do not appear to benefit greatly from increased social interactions. For example, inter-specific grooming and play were very infre-

quent, although huddling was more common. The lack of inter-specific grooming is in line with observations in the wild. However, the general raised level of social activity, and the fact that the two species attend and respond to each other's behaviour, may reduce potential boredom associated with restricted captive environments. Interestingly, one case of inter-specific sexual solicitation and mating was noted between the female red-bellied tamarin and the male saddle-backed tamarin. There are no accounts of such interactions in the wild, but HEYMANN and SICCHAR (1988) reported an inter-species copulation in their captive mixed-species tamarin troop. They describe a sub-adult moustached tamarin attempting to mate with a young saddle-backed tamarin, but regard this as "rare". We were unable to find any reports of hybridisation between saddle-backed tamarins and members of Hershkovitz' *mystax*-group in the literature (e.g. HERSHKOVITZ, 1977), suggesting that hybrids are behaviourally and/or physically prevented. Therefore these very rare attempts at copulation should not be seen as a cause for concern.

There are many factors affecting how successful captive primate mixed-species troops will be, and how much the individual animals, and the public will benefit from such exhibits. Individual and species temperament are two important considerations. Niche differentiation is also very important (DALTON and BUCHANAN-SMITH, in press), and success is often related to whether the species are sympatric in nature, as those that co-exist naturally are generally not in direct competition for the same resources. We would argue further that the most successful mixed-species exhibits will be with those species that also form stable associations in the wild.

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Author's address:

Scott M. Hardie: Division of Psychology, School of Social & Health Sciences, University of Abertay Dundee, Dundee DD1 1NJ, UK. E-mail: S.Hardie@abertay.ac.uk

Mark J. Prescott: RSPCA, Wilberforce Way, Southwater, Horsham, West Sussex, RH13 9RS, UK.

Hannah M. Buchanan-Smith: Department of Psychology, University of Stirling, Stirling, FK9 4LA, UK.

INFLUENCES OF MANTLED HOWLERS (*ALOUTTA PALLIATA*) ON FEEDING PATTERNS OF RUFOUS-NAPED TAMARINS (*SAGUINUS GEOFFROYI*): AN EXPERIMENTAL STUDY. RASMUSSEN, D.R. AND BROEKEMA, I.

Key words: Interspecies interactions, competition, mixed species, feeding, vertical space, ecology, sympatric

Abstract

Many correlational studies have been conducted on mixed species primate groups and sympatric species, and evolutionary theory has been advanced to understand interspecies interactions. However, few experimental field studies have been conducted to determine causal influences of one primate species on another. In this paper, we describe an experimental field study focused on the effects of mantled howler monkeys (*Alouatta palliata*) on rufous-naped tamarins (*Saguinus geoffroyi*). Two juvenile howler monkeys were placed on a small island with 5 tamarins in an A₁-B₁-A₂-B₂ experimental design: A₁-baseline with no howlers present, B₁-experimental condition with howlers present, A₂-second baseline with no howlers, and B₂-second experimental condition with howlers present. Systematic focal sample data were collected on the tamarins' feeding patterns, their height in the forest, their distance from the nearest howler, the height of the howlers, and agonistic interactions between the two species. The presence of the howlers appeared to slightly decrease the tamarins' rate of feeding on provisioned and natural food. This effect diminished during the second experimental condition. There were few agonistic interactions between the species and no wounding or deterioration in the condition of either species was observed. The tamarins shifted early morning and mid-day feeding patterns later when the howlers were present. There was a faint tendency for the tamarins to be higher in the trees when the howlers were present. Analyses of the relationships between the variables suggest the tamarins and the howlers were simultaneously attracted to the same provisioned and natural food items. This led to synchrony in their use of vertical space. Early in the day, when provisioned food was more frequently accessed, the tamarins and howlers tended to be closer to each other. The two species did not seem to form a mixed species group; instead, they were drawn together by use of common resources. The introduction of the howlers to the island was deemed a success as neither species appeared to be compromised by the presence of the other. It is possible that that they could both profit from sharing the same island since they could alert each other of the presence of potential dangers and resources.

Introduction

Previous field studies on mixed species groups have been correlational or differential (in the sense of GRAZIANO and RUALIN, 1997) research: interactions and relationships between two or more species are either qualitatively or quantitatively described (e.g. TERBORGH, 1983). Therefore the causal influence of one species on another can only be inferred: despite intricate evolutionary theory, one species can seldom be definitively said to have either a positive or negative impact on the other

whether through access to food or in the avoidance of predators. Such causal analyses are more firmly supported with experimental studies (GRAZIANO and RUALIN, 1997).

In the field experiment reported here, two mantled howler monkeys (*Alouatta palliata*) were introduced onto a small island where a group of five rufous-naped tamarins (*Saguinus geoffroyi*) lived (We prefer the common name rufous-naped (MOYNIHAN, 1970) to red-crested (SNOWDON and SOINI, 1988) because the back of the neck is rufous or mahogany in color and this coloration is quite distinctive. On the other hand, the species does not have a red-crest on the top of its head. The top of its head is white (Fig. 1). In this paper, we report the influences of the howler monkeys on patterns of the tamarins' use of food, vertical space and time.



Fig. 1: Rufous-naped tamarin (*Saguinus geoffroyi*).
Photo by Dennis R. Rasmussen.

Tamarins and howlers are sympatric in portions of their natural habitat, such as on Barro Colorado Island, but seem unlikely to intensively compete with howlers when they are sympatric.

Mantled howlers consume a large proportion of leaves in their diet although they will eat fruit, they are therefore foliovores and frugivores (JOLLY, 1972). SNOWDON and SOINI (1988) classify tamarins as "insectivore- frugivores, with a tendency to omnivory". Tamarins typically occupy the mid- to lower-canopy levels of younger forests (RASMUSSEN, 1989) and howlers are most often found in the upper canopy of mature forests (JOLLY, 1972). While tamarins and howlers have not been observed to form mixed species groups in nature, they seem unlikely to be intense competitors. We therefore anticipated that placing howlers with the tamarins would not lead to intense conflict.

We hoped that, for reasons similar to the many theoretical advantages of mixed species groups, the combination of howlers and tamarins might be to their mutual advantage. For example, each species could alert the other of potential dangers such as the presence of predators, for example boa constrictors, omnivorous mammals such as opossums, and the occasional large hawk. Since the two species seemed un-

likely to compete intensively, placing them together seemed a good management practice: space available is increased and competition and conflict unlikely. Finally, we anticipated that each species might help "train" the other species to specialize in its own ecological niche. The howlers might train the tamarins to use more of the mid-canopy of the forest and the tamarins might train the howlers, by competition over fruit, to specialize more on eating leaves.

We used the A-B-A-B reversal design (BAER et al., 1968) for this experiment. The first baseline condition (A₁) assessed tamarin group structure without the howlers present. The first experimental condition (B₁) assessed this structure with the howlers present. The baseline condition (A₂) and experimental condition (B₂) were then repeated.

Methods

Study Area and Study Animals

The group of five tamarins that was the focus of this experiment lived on Tigrito II, a 2441 m² island located in Gatun Lake, Republic of Panama. This small and narrow island is 117 m in length and varies between a minimum of 10 m and a maximum of 35 m in width (BROEKEMA, 2002). A young adult female tamarin, "S", was first introduced onto the island on November 12, 1999. A 13-month-old male, "J", was then introduced two days later. During this experiment the female and male lived on the island with their three male offspring: twins ("P" and "D") aged 13 months and a 4 month old ("M"). Table 1 summarizes the information on the date of birth, gender, and the housing history of each of the tamarins and howlers. These were the only primates living on the island. The juvenile male howlers, "U", and the juvenile female "K", used in this experiment were chosen since they were gentle towards another group of tamarins with which they had lived for several months immediately before this study. Both species were habituated to the presence of observers and caretakers. When data collection was commenced, observation teams could approach as close as 10 m to the tamarins and the howlers. Data were collected from a distance of about 10 to 20 m from the focal subject.

Table 1: Age, gender and history of the tamarins and the howler monkeys.

Species	Animal ID	Date of Birth	Approximate age at beginning of experiment	Gender	Previously Captive
<i>Saguinus Geoffroyi</i>	S	unknown	estimated to be 3 years of age	female	yes
	J	October 10, 1997	3 years and 9 months	male	No, mother had been in captivity, father had not
	P	May 30, 2000	13 months	male	no
	D	May 30, 2000	13 months	male	no
	M	March 6, 2001	4 months	male	no
					P, D and M are offspring of S and J
<i>Alouatta palliata</i>	U	October 2000	9 months	male	yes
	K	October 2000	9 months	female	yes

Three tamarins were marked so all individuals could be clearly identified by observers. A ball chain collar with a single red macramé bead was placed around "S"'s neck, and a ball chain collar with an aluminum macramé bead was placed around "J"'s neck. In order to distinguish between the twins, the central 2 cm of "P"'s tail was shaved several days before initiation of data collection. The youngest tamarin, "M", could be distinguished from "D" by his smaller size.

Most of the secondary forest on the island is about 60 years of age as the island was partly cleared during World War II. Fruit bushes and trees provide food for the tamarins and howlers. The tamarins successfully foraged for insects and other arthropods. The natural food was enhanced with seven sliced bananas every morning during the baseline conditions and, when the howlers were present, with 14 sliced bananas. The bananas were placed on a wire mesh screen about 40 by 40 cm square and mounted 1.5 m above the ground on a tree. There were always a few slices of banana left by the end of the day throughout the study. As there was an abundance of leafy vegetation, it is probable that the howlers could have survived without the provisioned food. However, the tamarins probably had to have the ripe fruit, as there is not an abundance of such fruit on the small island. Both species had fed on bananas extensively when young and for both species, ripe bananas were a favorite food source.

Sampling Methods

The data were collected by three teams of four observers working in three sequential shifts. The shifts were from 7:00 AM to 10:40 AM, from 10:40 AM to 2:20 PM, and from 2:20 PM to 5:40 PM. Teams were moved up a shift each day so each team collected data during a different shift every day. Sampling sessions were conducted for 30-min on focal subjects (MARTIN and BATESON, 1993). The tamarins were sequentially sampled from a list of the five group members. The subjects were sampled at different times across shifts and days.

Variable Definitions

All sampling was based on two min intervals signaled by an audible tone from the laptop computer used to record the samples.

Instantaneously Sampled Distance Variables

Instantaneous samples were taken once every two minutes on the focal subject height, distance to the nearest howler and the height of the nearest howler. Howler distances and heights were only recorded when the nearest howler was within 20 m of the focal subject. Height was defined as the distance between the animal and the ground (or water) below. The scale used to estimate height is as follows: 0-2m = 0, 2-4m = 2, 4-6m = 4, 6-8m = 6, 8-10m and greater = 8. Nearest howler distance was the straight-line distance between the focal tamarin and the nearest howler estimated to the nearest meter.

Frequency Sampled Variables

Frequency sampled variables were recorded every time they occurred during a given 2 min interval.

Eating provisioned food was recorded when the focal subject placed a piece of banana in its' mouth, chewed it, and apparently ingested it. Eating food that was not provisioned was recorded as eating natural food. Eating natural food was recorded when the subject placed an object in its mouth, chewed it and apparently ingested it. Intervals used to calculate rates of feeding were discarded if the focal subject was not visible. Frequencies of feeding were converted to rates by dividing summed frequencies by the number of valid 2 min intervals. Rates are therefore number of times eating provisioned or natural food was observed to occur per valid 2 min interval.

The agonistic variables were always recorded when they involved the focal subject. If time and conditions permitted, concurrent sampling (RASMUSSEN, 1995) was also conducted on all tamarins and on the howlers. Supplants were recorded when one individual approached within 5 m of another and stopped for at least 5 s and the approached individual moved away within 5 s after being approached. Chases were recorded when one individual ran after another who was actively attempting to escape from that individual. Bites were recorded when one individual closed its teeth on another and the bitten individual attempted escape.

Data Management and Analysis

Data were uploaded from the laptop to a desktop computer for editing within 24 hours of collection. SPSS 10 FOR WINDOWS (2000) was used for file management, data description and analysis.

Experimental Design

The first baseline, A₁, was conducted before the howlers were introduced. The first experimental condition, B₁, was conducted with the howlers present. The second baseline, A₂, was conducted after the howlers were removed, and the second experimental condition, B₂, was conducted after the howlers had been reintroduced. Four days of data were collected during each condition. On the first day of each experimental condition, the howler monkeys were placed on the island a few minutes before initiation of data collection. The howlers were removed a few minutes before the initiation of data collection on the first day of the second baseline, A₂. The conditions of the experiment, the dates of data collection and number of 2-min intervals of data collected during each day are summarized in Table 2.

Table 2: Conditions of the experiment, cumulative days the tamarins were observed, month and day of data collection, and number of 2-min intervals of data collected each day.

Condition	Days Observed	Month	Day	2-minute Intervals
A ₁ First Baseline Condition	1	6	28	217
	2	6	29	260
	3	7	1	268
	4	7	2	266

Condition	Days Observed	Month	Day	2-minute Intervals
B ₁ First Experimental Condition	5	7	3	249
	6	7	4	270
	7	7	5	175
	8	7	6	242
A ₂ Second Baseline Condition	9	7	9	240
	10	7	10	270
	11	7	11	254
	12	7	12	256
B ₂ Second Experimental Condition 4	13	7	13	258
	14	7	16	270
	15	7	17	269
	16	7	18	241

Statistical Analyses and their Interpretation

We analyze data that are both experimental and non-experimental in this study. The only data that are truly experimental are the comparisons between the baselines and the experimental conditions. These show the causal effects of the manipulated variable, presence or absence of the howler monkeys, on the dependent variables, aspects of the feeding behavior and use of vertical space of the tamarins. Our non-experimental analyses focus on patterns of interactions and spacing between the tamarins and the howler monkeys. These relationships between the tamarins and howlers can only be analyzed within the experimental conditions when the howlers were present. We use these non-experimental and correlational analyses to determine possible proximate causes of the experimental results.

This is a repeated measure experiment conducted on a single entity, a group of tamarins. As in classic applied behavioral analysis (BAER et al., 1968), we rely on descriptive statistics and graphical analyses. There is a long and complex history in the philosophy of science focused on single subject experiments (IWATA et al., 2000). Briefly, the goal of experiments is to prove cause and the A-B-A-B single subject design used here can show systematic manipulation of the experimental variable has a causal influence on dependent variables. Increased confidence in the results of single subject designs comes about when those results are replicated, as in all experimental studies.

We also use correlation analyses of relationships between variables within the experimental condition. We stress that these correlational analyses are descriptive. Like the mean and variance, a correlation coefficient is a descriptive statistic of the strength of the linear relationship between two variables. These correlations are not tested for significance, as the standard test of significance of the Pearson Product-Moment Correlation Coefficient is inappropriate (COHEN and COHEN, 1983). We use scatter diagrams to graphically show the relationships between two variables.

Results

The tamarins' rate of feeding on both provisioned and on natural foods decreased during the experimental conditions (Figures 2 and 3). Reference to the mean rates of feeding on these figures reveals a distinct A-B-A-B pattern. There was, however, considerable daily variation in rates of feeding, particularly in rates of feeding on natural food.

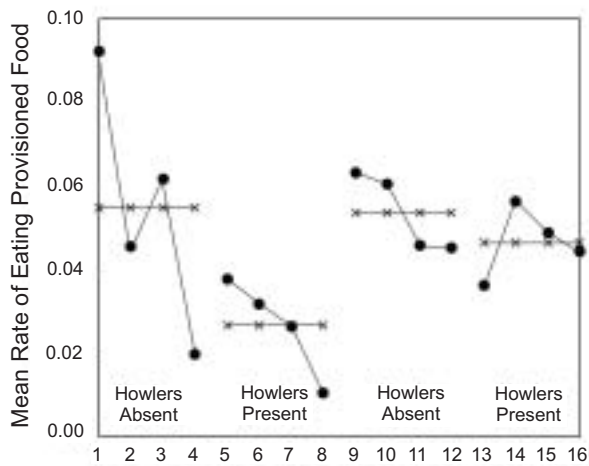


Fig. 2: Tamarins' mean rates of eating provisioned food decreased when the howlers were present.

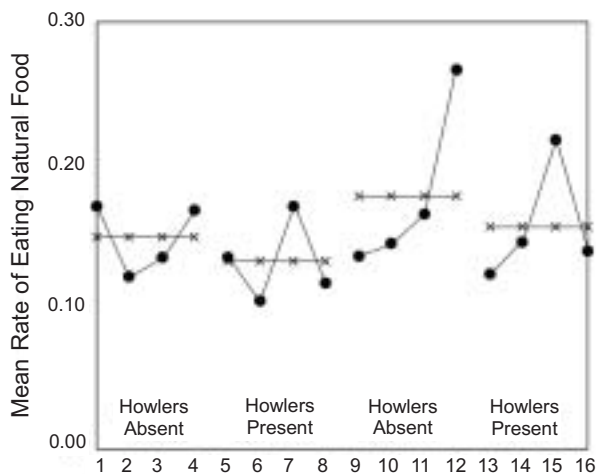


Fig. 3: Tamarins' mean rates of eating natural food decreased when the howlers were present.

The amount of difference between rates of eating provisioned food during the second baseline and the second experimental condition decreased compared to the difference between first baseline and first experimental condition. The tamarins actually ate natural foods at a higher rate during the second experimental condition than during the first baseline. It appears, then, that the tamarins were becoming habituated to the presence of the howlers and the howlers had a less marked influence on

tamarins' rate of feeding on provisioned food by the end of the second experiment. The tamarins may have also slightly increased their rate of eating natural food.

Previous analyses have indicated that the tamarin group tended to become more spatially compact when the howlers were present (RASMUSSEN et al., 2002). This result suggests the tamarins initially responded to the howlers as a potential danger, since groups of many species tend to become more compact when faced with a potential danger, such as a predator (HAMILTON, 1971).

The tamarins were more aggressive toward the howlers than the howlers were to the tamarins. There were, however, exceptionally few agonistic interactions between the howlers and the tamarins. The howlers supplanted the adult female three times, and once chased a juvenile tamarin. The tamarins were observed to chase the howlers 6 times. There was an equal amount of agonistic behavior during the first and the second experimental conditions. No wounds or any indication of injuries were observed on either species. All individuals of both species appeared in excellent condition throughout the entire study.

The decreased rates of feeding when the howlers were present suggests the howlers had a slight negative impact on the tamarins' feeding, even though there was a very low rate of aggressive conflict between the two species. The presence of the howlers might depress the tamarins' rates of feeding in several ways. For example, the tamarins may have been avoiding the howlers and hence ate less frequently. Alternatively, they may have been more vigilant and focused on the behavior and locations of the howlers and hence ate less frequently. We reasoned that if the howlers' presence influenced feeding rates, then this influence might be revealed when the howlers were closer to the tamarins. We therefore analyzed rates of feeding of the focal tamarin as a function of the distance of the nearest howler.

As is indicated in Figures (4 and 5), the tamarins tended to eat both provisioned and natural foods at higher rates when the howlers were closer. These results seem likely to indicate that both the tamarins and howlers were attracted to the same provisioned and natural food sources at the same time and hence tended to have a

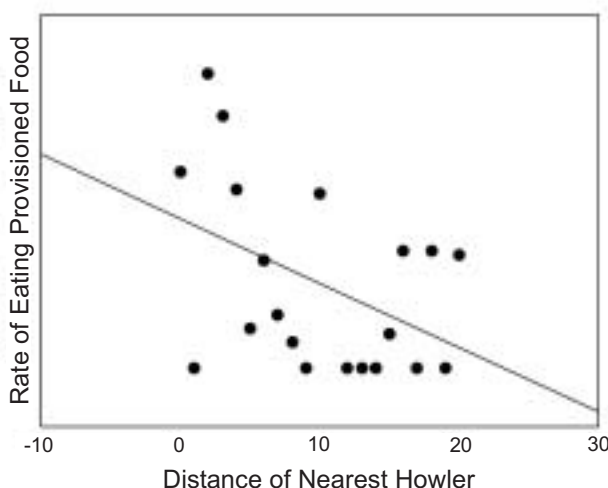


Fig. 4: Rate, per 2 min interval, of eating provisioned food per day as a function of the distance of the nearest howler monkey to the focal subject. Focal tamarins tended to eat provisioned foods at higher rates when the howlers were closer ($r = -.44$).

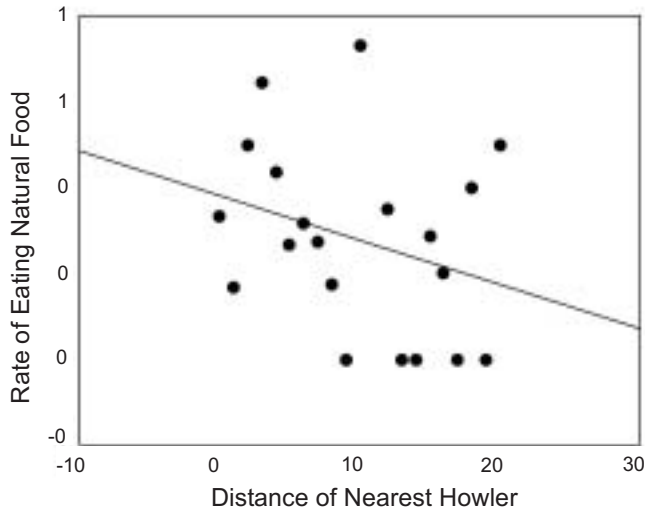


Fig. 5: Rate, per 2 min interval, of eating natural food per day as a function of the distance of the nearest howler. Focal tamarins had a weak tendency to eat natural foods at higher rates when the howlers were closer ($r = -.30$).

higher rate of using both provisioned and natural food sources when the other species was near by. Note that if we did not have the previous experimental results, it could easily be argued that the howlers were facilitating the tamarins' ability to find food: when close to the tamarins, the tamarins ate at higher rates. Because rates of feeding were depressed during the experimental conditions when the howlers were present, this interpretation becomes difficult to maintain.

The height at which the tamarins and howlers were closest, might indicate the location of the food source over which competition was most intense. Analyses of the data indicated that the nearest howler monkey tended to be closer to the focal tamarin when the tamarin was lower in the vegetation ($r = +.70$, Figure 6). If a decreased distance between the tamarins and howlers was associated with competition for food, then it appears that there was more competition over food near the ground,

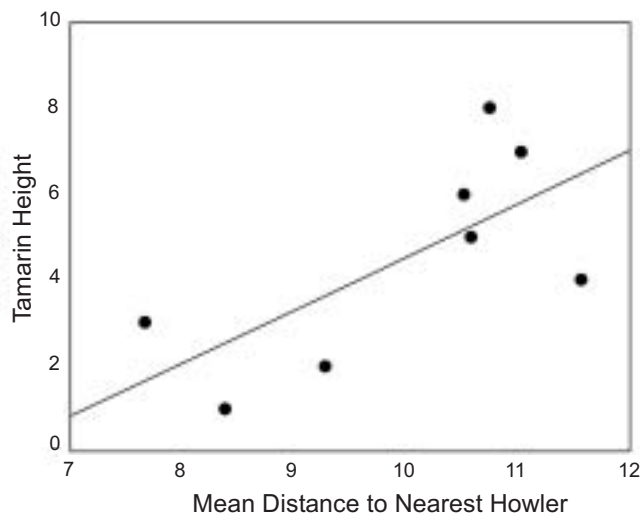


Fig. 6: Focal tamarins' height plotted as a function of their mean distance to the nearest howler. Tamarins tended to be lower in the vegetation when the howlers were closer. There was a substantial correlation between the height of focal tamarin and mean height of nearest howler ($r = +.70$).

such as at the provisioning tray, rather than higher up in the trees. It is also possible to look at the height of the nearest howler as a function of the distance of the nearest howler from the focal tamarin. These analyses show where the howlers were in vertical space when they were close to tamarins. Again, there is a strong positive relationship: The closer the howler to the focal tamarin, the lower was the howler ($r = +.79$, Figure 7).

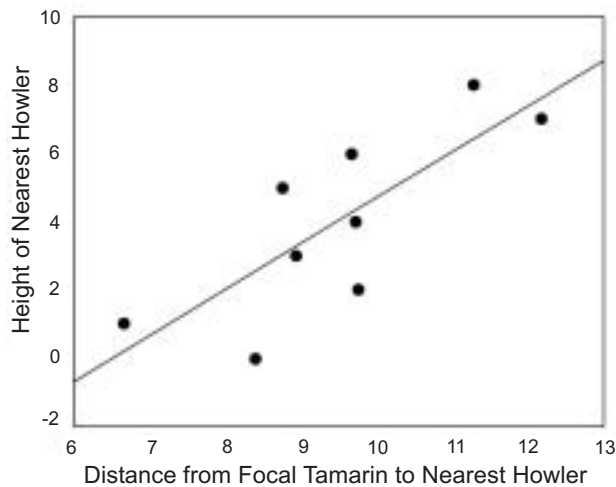


Fig. 7: Height of howlers as a function of their mean distance to the nearest focal tamarin. As with the tamarins, there was a substantial tendency for howlers to lower when they were closer to the focal tamarins ($r = +.79$).

As tamarins were closer to the ground when howlers were near and howlers were closer to the ground when near tamarins, this suggested that the tamarins and howlers tended to be at similar heights at the same time. Figure 8 shows that the mean height of focal tamarins was associated with the height of the nearest howler ($r = +.67$).

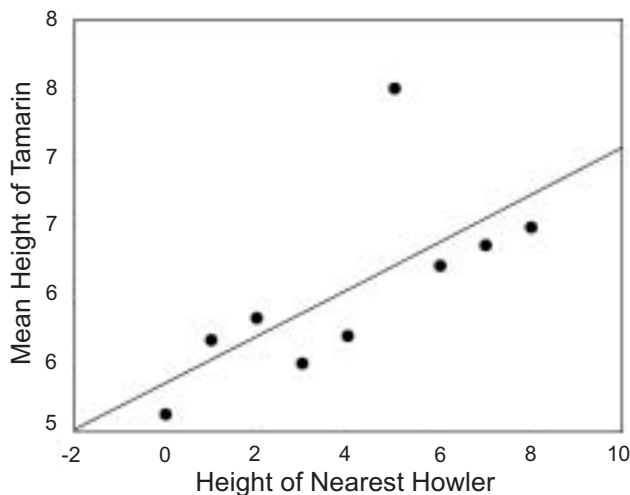


Fig. 8: Mean height of focal tamarin subject plotted as a function of the height of the nearest howler. As suggested by the previous two figures, tamarins and howlers tended to be at the same heights at the same times ($r = +.67$).

While apparently at odds with the natural history of the two species, examination of figure 8 shows that when the howlers were near the ground, less than 6 m in height, they tended to be lower than the tamarins. This pattern could be a result of the former captivity of the howlers. At the height of 6 m and greater, the tamarins and howlers tended to be at the same height. When the howlers were high up in the trees, the tamarins also were more frequently high and when the howlers were on the ground, the tamarins tended to be closer to the ground.

Both the tamarins and the howlers therefore tended to be closer to each other when lower in the vegetation and they paralleled each other throughout the day in their vertical height. If competition and avoidance were associated with proximity and feeding, then it would seem likely that the presence of the howlers might influence the tamarins' height in the vegetation. The somewhat surprising results shown in Figure 8 suggest that if the tamarins avoided the howlers, they might ascend higher into the vegetation since the howlers tended to be lower than the tamarins. A comparison of the heights of the tamarins during the baseline and experimental conditions did reveal a weak A-B-A-B pattern (Figure 9). The tamarins had a slight tendency to be higher when the howlers were present. However, the actual change in the average height of the tamarins was less than 10 cm and there was a great deal of variability across days within each condition.

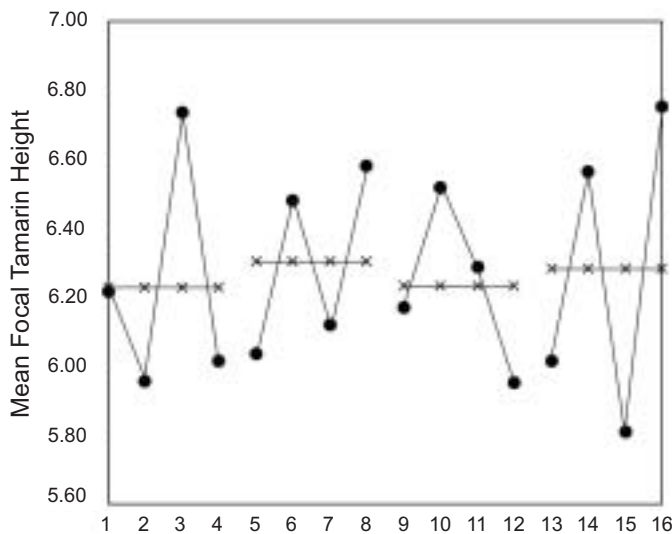


Fig. 9: Tamarins tended to have a slightly greater mean height during experimental phases. The large amount of variation and small differences in means make these results suggestive at the most.

Patterns of feeding were associated in height; it seemed probable that they were also associated in time. An analysis of the relationship between the hour when a sampling session was initiated and the mean distance to the nearest howler confirmed this possibility: Tamarins were closest to howlers earlier in the day ($r=+.80$, Figure 10). Provisioned food was placed on the platform about 7AM before the initiation of data collection. The tamarins and howlers tended to drift apart as the day wore on. The provisioned food and possibly high quality natural foods again seem likely to have drawn the two species together. We checked this possibility with analyses of the relationships between the hour during which sampling sessions were ini-

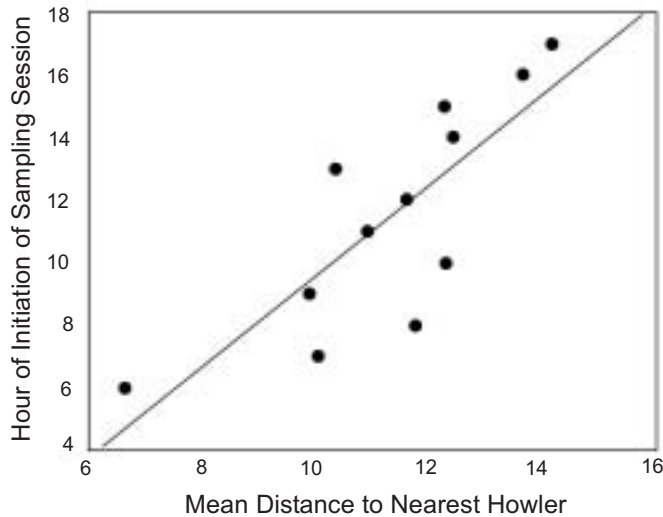


Fig. 10: The hour when sampling sessions were initiated are plotted here as a function of the mean distance of the focal tamarin to the nearest howler. Tamarins and howlers had a strong tendency to be closer to each other early in the day and drift farther apart as the day wore on ($r=+.80$).

iated and rates of feeding. We found a substantial correlation between the rate at which focal subjects ate provisioned food and the hour during which the sampling session on those subjects were initiated ($r = -.61$): tamarins ate provisioned food at higher rates earlier in the day (Figure 11). There was no relationship between the rate of eating natural food and the hour sampling sessions were initiated ($r = -.09$).

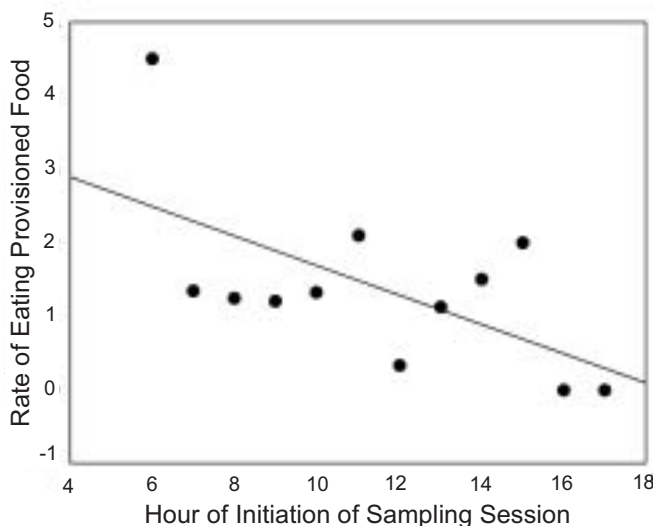


Fig. 11: The focal subjects' rate of eating provisioned food is plotted here as a function of the hour of initiation of sampling sessions. There was a substantial tendency for the tamarins to eat more provisioned food earlier in the day ($r = -.61$). There was no relationship between rates of the focal subjects eating natural food and the hour of initiation of sampling sessions ($r = -.09$).

It was possible to analyze how the presence or absence of the howlers influenced the time at which the tamarins fed. Figure 12 shows the difference in the rate at which the tamarins ate provisioned food during the baselines and experimental conditions. A positive value indicates the tamarins ate at a higher rate at a given hour of

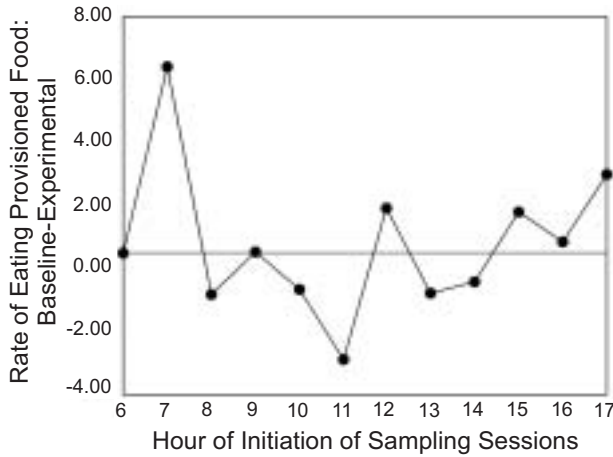


Fig. 12: The difference between the rate of eating provisioned food during the baselines and the rate of eating provisioned food during the experimental conditions is graphed here as a function of the hour during which sampling sessions were initiated. Values above the zero line indicate a higher rate during the baselines whereas values below the zero line indicate a higher rate during the experimental conditions. The graph shows that the presence of the howlers shifted morning feeding time and mid-day feeding times later for both provisioned and natural foods.

the day during baseline sampling sessions in comparison to during the experimental sessions, a zero value indicates no difference, and a negative value indicates a higher rate during the experimental conditions. The tamarins had a higher rate of feeding on provisioned food early in the morning, between 6 and 8 AM during the baseline periods. This was when the food was first placed on the food tray. The tamarins also had a higher rate of feeding during the baselines between 11AM and 1PM. During the experimental conditions, there was a partial shift toward later morning and later early afternoon feeding in the tamarins. These same patterns are apparent in the rates at which the tamarins ate natural food (Figure 13).

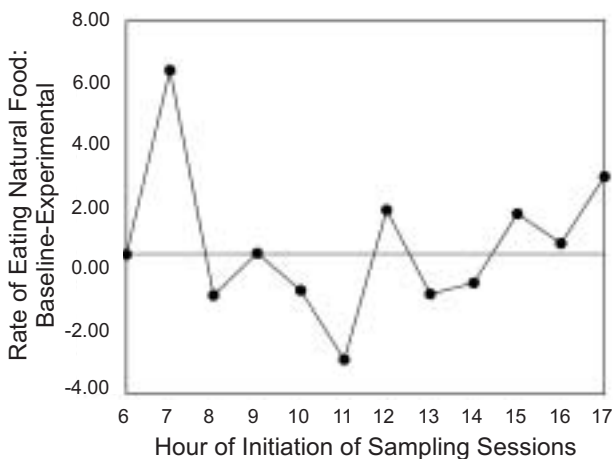


Fig. 13: The difference between the rate of eating natural food during the baselines and the rate of eating natural food during the experimental conditions is graphed here as a function of the hour during which sampling sessions were initiated. Values above the zero line indicate a higher rate during the baselines whereas values below the zero line indicate a higher rate during the experimental conditions. The graph shows that the presence of the howlers shifted morning feeding time and midday feeding times later for natural foods.

Discussion

The following is a summary of the rather complicated results of the experimental and non-experimental analyses:

Experimental results: Possible causal influences of the presence of howlers on tamarins:

- Rates of feeding on both provisioned and natural food were depressed when the howlers were present.
- Morning and midday bouts of feeding on both provisioned and natural foods were delayed when the howlers were present.
- Tamarins had a tendency to be higher when the howlers were present.
- No visible wounds or deterioration in the condition of tamarins when the howlers were present.

Non-experimental results: Analyses of relationships between howlers and the tamarins

- The tamarins tended to eat both natural and provisioned food at higher rates during the experimental conditions when the howlers were closer.
- Tamarins were closer to the ground when howlers were near and howlers were closer to the ground when near tamarins.
- Tamarins and howlers tended to be at similar vertical heights.
- Howlers tended to be slightly lower than the tamarins.
- Tamarins were closer to howlers earlier in the day.
- Tamarins' rates of feeding on provisioned food tended to be higher early in the day but there was no trend in rates of feeding on natural food associated with time of day.

The analyses indicate that the howlers had an influence on the tamarins and the two species were responsive to the presence of each other. The experimental data are least equivocal: First, the howlers' presence slightly depressed tamarins' mean daily rates of feeding on provisioned and natural food. This effect decreased by the end of the second experimental condition. Second, the presence of the howlers was not associated with an increase of wounds or deterioration in the visible condition of the tamarins. Third, there was a slight tendency for the tamarins to be higher when the howlers were present. Fourth, the morning and midday bouts of feeding were delayed when the howlers were present.

The changes in rate of feeding on provisioned food decreased between the second baseline and second experimental condition. For both provisioned and natural food, there was little difference between the first baseline and the second experimental condition. There was actually a slight increase in the rate at which the tamarins ate natural food during the second experimental condition above the rate during the first baseline. The tamarins appeared to habituate to the presence of the howlers (RASMUSSEN et al., 2002). Spreading out the provisioned food across several widely separated platforms might ameliorate the slight change in rates of feeding.

The shift in timing of bouts of feeding does not have an immediately apparent negative aspect. Studies of the likelihood of encounter with various species of preda-

tors as a function of time of day might indicate the time shift had either a positive or a negative impact on the tamarins.

The absence of visible wounds or deterioration in condition, the first signs often looked for when newly forming groups of primates, suggest the introduction to have been successful. This judgment was born out by subsequent observation. The howlers were left on Tigrito II with the tamarins after the termination of the second experimental condition. At the time of this writing, over a year since the study was initiated, no wounds have been seen on either the tamarins or the howlers and no aggressive physical contact has been observed between the two species. New offspring were born to "S" and "J" on October 19, 2001. We feel that the introduction of the howlers was a success. Tigrito II is now populated with both tamarins and howlers and the two species appear to be thoroughly accustomed to each other.

The non-experimental results help in the interpretation of the experimental effects. The tamarins tended to eat both provisioned and natural foods at higher rates when the howlers were near. We interpret these results to indicate that the howlers and tamarins tended to use some of the same high quality provisioned and natural food sources. The tamarins seem likely to have eaten at higher rates when the howlers were near because the howlers were near when they were using high quality food sources.

The two species did not overtly avoid each other, rather the data indicate they tended to have parallel use of vertical space: When the tamarins were close to the ground so were the howlers.

The analyses indicate the two species tended to be closer to each other earlier in the day and that the tamarins ate more provisioned food early in the day. Together these results suggest that the provisioned food was a powerful factor in drawing the two species together. Previous studies have documented that provisioned food can draw primate species together (WRANGHAM, 1974). Qualitative observations suggested both species would also sometimes approach the observers and thereby approach each other.

The tamarins may have moved up slightly in height when the howlers were present. We actually anticipated the howlers might move them down from the upper canopy where the howlers have been most frequently observed in field studies. Instead, the howlers may have increased the tendency for the tamarins to ascend up higher after they took a slice of banana from the food tray. The howlers did, at times, sit directly on the food tray and eat their fill of the bananas. This did not prevent the tamarins from taking a slice, but it did prevent them from sitting on the food tray as they did when the howlers were not present. We feel this effect of the howlers' presence was positive: the tamarins are most likely safer in the lower branches of trees than on the feeding platform. It is probable that the presence of the howlers also slowed down the rate at which the tamarins could feed and this may have been partially responsible for shifting bouts of feeding to later in the day during the experimental conditions.

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Correspondence to:

The Primate Foundation of Panama, Apartado 2023, Balboa-Ancon, Republic of Panama. E-mail: pfp@primatesofpanama.org