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MIXED-SPECIES EXHIBITS WITH MAMMALS IN CENTRAL EUROPEAN ZOOS

BY CAROLINA PROBST AND CHRISTIAN MATSCHEI

Introduction

Interactions between different animal species are common in wildlife, ranging from chance encounters to permanent associations. They may be the result of cooperative breeding, common migration, using the same habitat, or exploiting clumped resources like food, water, minerals, sleeping berths or hibernation sites (Deegener, 1918; Morse, 1977; Kratochwil and Schwabe, 2001). Functional explanations for heterospecific associations have been particularly studied in primates (Stensland *et al,*, 2003; Boinski and Garber, 2000; Terborgh, 1990; Struhsaker, 1981). The main evolutionary benefits include complementary vigilance and increased access to food.

Zoo animals, especially primates, ungulates and birds, are increasingly kept in mixed-species associations as well. Nevertheless, the reasons for housing animals in heterospecific groups in captivity are different from the reasons for such associations in wildlife. Mixed-species exhibits are considered to be an important form of behavioural enrichment, provide a better educational experience for the visitor, and have economic advantages. On the other hand, animals in mixed-species exhibits are exposed to more hazards than in single-species exhibits. Unfortunate outcomes might include stress, trauma, diseases, and death.

Mixed-species associations in wildlife

The main benefits for an individual animal of associating with others include (1) predator avoidance and (2) feeding advantages. Furthermore, in mixed-species associations reproductive competition is reduced, and resource competition is generally less than in single-species associations (Dickmann, 1992).

(1) Reduced risk of predation

By associating with other animals (of other species), individuals improve their survival chance. First, a high number of animals reduces the per capita risk of being chosen as prey (dilution effect). Second, group vigilance and therefore the likelihood of detecting predators in time is increased (detection effect). Third, choosing and attacking a specific prey is more difficult (confusion effect) (Krebs and Davies, 1997). Heterospecific attraction has been shown in birds (Forsman *et al.*, 2002), in fishes (Mathis and Chivers, 2003; Landeau and Terborgh, 1986; Itzkowitz, 1977) and in invertebrates (Hodge and Uetz, 1992). Among mammals, heterospecific groups in order to reduce predation risk are especially common among primates (Cords, 1990). For example, at Cocha Cashu in Peru, squirrel monkeys benefit from the warning system of capuchin monkeys (Terborgh, 1985). In the Taï National Park, Ivory Coast, red colobus monkeys and diana monkeys profit from each other's predator avoidance behaviour: the colobus monkeys draw attention to predators from above (i.e. from the air), and the diana monkeys draw attention to predators from the ground (Höner *et al.*, 1997; Noë and Bshary, 1997). Two species of New World tamarins, *Saguinus mystax* and *S. fuscicollis*, associate for the same reason: the first are alert to hazards from above, the latter to hazards from below (Peres, 1993; Smith *et al.*, 2004). In the Serengeti National Park, Tanzania, Thomson's gazelles and Grant's gazelles are less vulnerable to cheetah when associated in mixed-species groups (Fitzgibbon, 1990). Based on the suggestion of Sinclair (1985), Burchell's zebras reduce their risk of predation by staying close to blue wildebeest, the favourite prey of large predators in the Serengeti. Another example are Cape ground squirrels (*Xerus inauris*), which inhabit burrows together with meerkats. The squirrels spend less time alert and more time feeding when the meerkats are present. In return, the meerkats benefit from the burrowing activities of the squirrels for thermoregulation and to escape from predators (Waterman and Roth, 2007). The use of burrows of other rodents by birds is well known, but the possible costs and advantages have been poorly studied.

(2) Increased feeding success

Heterospecific associations for the purpose of increasing foraging efficiency have been recorded in several vertebrates:

Associations of different species of mammals. Commensal feeding relationships between mammals are not particularly common. They have been recorded between different primate species (e.g. Höner *et al.*, 1997; Waser, 1987) and between primates and ungulates. For example, bushbucks preferably stay near baboons, as these drop large quantities of leaves, seeds and fruits onto the ground while foraging on the trees. Thereby, the bushbucks can exploit an additional source of energy otherwise unavailable, and in addition they profit from the alarm calls of the baboons (Elder and Elder, 1970). Sika deer are thought to gain the same sort of benefit by associating with Japanese macaques (Majolo and Ventura, 2004), and impalas by associating with baboons (Morgan-Davies, 1960). Similarly, the excavating activities of aardvarks on termite nests could be of considerable benefit to aardwolves: associative feeding between both has been observed by Taylor and Skinner (2000). Again, heterospecific associations in order to increase feeding success exist between California sea lions and two dolphin species (*Tursiops truncatus* and *Delphinus delphis*) (Bearzi, 2005), as well as between several species of fish and dolphins (Sazima *et al.*, 2006).

Associations among mammals and birds. Some birds achieve a higher rate of energy intake by associating with mammals. Association with reindeer permits snow grouse to exploit the vegetation shovelled free from snow by the deer (Schaefer, 1992, p. 433). Insectivorous birds may take advantage of the prey-flushing effect of mammalian activity. For example, in the Taru desert in Kenya the two hornbill species *Tockus flavirostris* and *T. deckeni* profit from the foraging activities of dwarf mongooses by snapping up the disturbed jumping and flying insects (Rasa, 1983). Another possibility is to feed on mammalian ectoparasites. One of the most famous examples is that of the oxpeckers (*Buphagus* spp.), closely related to the starlings, which groom ticks from the ears, noses and genital areas of elephants, rhinos, antelopes and other bovids. Jacanas (*Actophilornis africana*), Hartlaub's ducks (*Cairina hartlaubi*) and finfeet (*Podica senegalensis*) pick arthropods from the skin of forest buffalo and bongos. The birds profit from an abundant food resource, and the hoofed mammals are relieved of discomfort and possibly of arthropod-borne diseases. They also profit from the early alarm calls of the birds (Ruggiero and Eves, 1998).

Mixed-species exhibits in zoological gardens

Mixed-species exhibits are becoming increasingly popular in zoological gardens (Thomas and Maruska, 1996). Therefore, new combinations are continually being tried out. Three Taxon Advisory Groups (TAGs) have collected some examples from North American zoos: the Antelope TAG, the Pig, Peccary and Hippo TAG, and the Rodent, Insectivore and Lagomorph TAG. (The lists are available on their respective home pages.) Furthermore, a symposium on the topic 'mixed-species exhibits of primates' was held at Dallas Zoo in 1999, and veterinary aspects of mixed exhibits were discussed at the Sixth Conference on Zoo and Wildlife Nutrition in 2005. Mixed-species displays in North American zoos are often designed to accommodate as many as 30 or more animals of different species. On the other hand, mixed exhibits in Central European zoos are usually much smaller and include fewer individuals of only two to four species. One of the largest mixed exhibits is the African Savannah at Zoom Erlebniswelt Gelsenkirchen, Germany, which successfully combines elands, greater kudus, roan antelopes, springboks and Grant's zebras with birds such as ostriches, griffon vultures, marabou storks and helmeted guinea fowl.

As regards experiences with mixed exhibits in European zoos, a growing number of papers have been published since the 1960s. Early experiences were described by Backhaus and Frädrich (1965) from Frankfurt Zoo, Germany, and Dittrich (1968) from Hannover Zoo, Germany. The founder of Boras Djurpark, Sweden, describes his gradual approach to associating African elephants with Grant's zebras, gnus, white rhinos, giraffes and ostriches (Berggren, 1969). Hammer (2002) compiled a worldwide survey of mixed exhibits with mammals and Ziegler (2002) one of mixed exhibits with primates in Germany. Other possible species combinations are elucidated in the book of zoo animal husbandry by Puschmann (2004). The topic 'mixed exhibits' is also the subject of a diploma thesis by Linnenberg (1994). Anecdotes based on experiences or intuitions of single authors are increasingly published in less scientific sources (e.g. **www.tiergarten.com**, 2006). But despite the vast amount of literature, the correct interpretation and generalisation of single events can still prove to be difficult (Damen, 2007).

Advantages of mixed-species displays

The reasons for heterospecific associations in the wild and in zoos obviously differ from each other. In a zoo, it is the responsible staff that make the decision which animals should be mixed when, where and in what configuration. The advantages of exhibiting different species in the same enclosure include (1) behavioural enrichment for the animals, (2) educational benefits and attractiveness for the visitors, and (3) management advantages.

(1) Ethological advantages

Mixed-species displays increase social complexity and therefore may provide behavioural enrichment for the animals. The following examples should illustrate this. At Schwerin Zoo, Germany, domestic goats nibble on the skin of the cohabitant white rhinos and provoke them into playing chasing games (Zscheile, 1999) (see also Table 1, No. 12). As shown in the photo (below), they also climb, ride and sleep on their backs. Similar behaviour could be observed in Safari Beekse Bergen in Hilvarenbeek, the Netherlands, where hamadryas baboons used to ride on African elephants and to groom them. Conversely, they were chased and splattered with water by the elephants (Deleu *et al.*, 2003). At Dortmund Zoo, Germany, South American tapirs would lie down with spread legs in front of the anteaters and invite them to lick their bellies, whereupon they might get beleaguered by several anteaters at the same time (Bartmann, 1980; Seitz, 2001) (see also Table 1, No. 31). A similar behaviour can be observed at Berlin Zoo, Germany, between capybaras and brocket deer (Nobert, 2001). At Gelsenkirchen Zoo an eland and a vulture have become so bonded that the eland regularly seeks the vulture to pick her fur (Gürtler, 2001) (see also Table 1, No. 32).

Pygmy goats riding on a rhino's back, Schwerin Zoo, June 2006. (Photo: Carolina Probst)

(2) Educational advantages

Some mixed exhibits offer the possibility to compare (a) similar-looking species (e.g. dromedary and Bactrian camel at Nuremberg Zoo, Germany), (b) different body parts like horns and antlers (e.g. fallow deer and mouflon at Schwerin Zoo), (c) adaptations to a specific habitat (African and Asiatic elephant at Augsburg Zoo, Germany) or (d) adaptations to an ecological niche (e.g. sable antelope with dik-dik or weavers with rock hyraxes). A zoogeographically correct composition is preferable, but is not an absolute condition – e.g. zebras, hartebeest, and Natal duikers at Landau Zoo, Germany (Honigs *et al.*, 2006); snowy owls and Arctic foxes at Dresden Zoo, Germany; collared peccaries and ring-tailed coatis at Liberec Zoo, Czech Republic (see Table 1, No. 61, and photo, below); musk deer and gorals at Edinburgh Zoo, United Kingdom. With some combinations, such as bongos and duikers at Burgers' Zoo, Arnhem, the Netherlands, information is needed in order to avoid the visitors' believing that the smaller species is the offspring of the bigger one.

Collared peccaries and coatis, Liberec Zoo, 2007. (Photo: Christian Matschei)

(3) Management advantages

The interest of zoo visitors is particularly attracted by interactions of different species (Smith and Tucker, 1999). For increased public interest, it is often sufficient to show different species eating or sleeping together. In this way, less impressive species can be promoted as well. Furthermore, mixed exhibits can provide accommodation for single males or other individuals which either live solitary or are not currently required to breed, e.g. tropical primate exhibits with agoutis or aviaries with lesser mouse deer. Cologne Zoo, Germany, houses a surplus group of male zebras with a family group of ostriches. At Berlin Zoo an old blind sea lion which was mobbed by its conspecifics lives together with common seals. Two solitary-living tamanduas are kept at Magdeburg Zoo, Germany, in separate enclosures, one of them with red-bellied tamarins and the other with common marmosets. Moreover, mixed enclosures allow an efficient use of space, especially if (a) the inhabitants occupy different ecological niches, e.g. orang-utans and Malayan tapirs at Dortmund Zoo, Germany (Burkhardt,

2006) or (b) the inhabitants have different day–night rhythms, like gorillas and genets at Heidelberg Zoo, Germany, or anteaters and maned wolves at Edinburgh Zoo.

Basel Zoo's male hippo Wilhelm defending his territory. Male zebra Kalungu is unimpressed, picking grass leftovers from between his teeth. (Photo: C. Hagen, July 2004)

Disadvantages of mixed-species exhibits

The possible risk of chronic stress, decreased breeding success, cross-contamination of infectious diseases and interspecific conflicts sometimes leads to the opinion that 'we are not doing the animals any favour by keeping them in association with other species' (B. Blaszkiewitz, pers. comm.; Walther, 1965). There follow some examples of these risks.

(1) Ethological disadvantages

The main source of difficulty in mixed-species exhibits is interspecific conflicts (Crotty, 1981; Popp, 1984). As mature males play a leading role in initiating aggressive interactions, in some cases they are only allowed to share the exhibit in a staggered way, e.g. the safari exhibit at Dvur Králové Zoo, Czech Republic, and the former exhibit with blackbucks and nilgais at Berlin Tierpark (this exhibit was eventually discontinued for other, unrelated reasons). Hence, sex ratios in these exhibits may not illustrate natural social groupings in the wild (Forthman *et al.*, 1995). Another approach to reduce male-initiated aggression in mixed-species exhibits is keeping bachelor groups, as for example Thomson's gazelles in Kiwara Savanne at Leipzig Zoo, Germany (Oberwemmer, 2004) (see also Table 1, No. 18) or the African exhibit at Hannover Zoo. Violent aggressive interactions, sometimes with a lethal outcome, may even occur after several years of problem-free coexistence, as in Basel Zoo, Switzerland: after 14 years living together, the Grant's zebra stallion was pulled into the water and bitten to death by the male hippo (see photo, p. 329, and Table 1, No. 40). A similar situation was reported from Krefeld Zoo, Germany, where a Chapman's zebra stallion was killed by a male eland (Encke, 1997). In the same zoo the combination of muntjacs and red pandas functions without problems, as long as there are no births. But newborns of each species have been killed by the other (Straube, pers. comm.). The same happens at Nuremberg Zoo: after coexisting and breeding for several years without problems, two muntjac fawns were killed by the red pandas (Mägdefrau, 2002). Leipzig Zoo successfully keeps sloth bears together with a troop of rhesus monkeys. As shown in the front cover photo, the bears even tolerate the monkeys riding on them. Nevertheless, after the monkeys teased them to excess, one of the bears eventually killed one of them (Eulenberger, pers. comm.). The risk of such incidents has to be taken into account especially if predators are mixed with potential prey, like meerkats with weavers (Ploceidae) at Berlin Zoo (see Table 1, No. 8), otters with trout at Zürich Zoo, Switzerland, or lions with mongooses and meerkats at Schwerin Zoo (Weidel, 2001) (see also Table 1, No. 44).

(2) Veterinary disadvantages

Mixed-species exhibits may lead to a higher level of stress, with resulting health problems like emaciation, self-mutilation and gastric ulcers (McAloose, 2004). Furthermore, the interspecies transmission of pathogens has to be taken into account (Lowenstine, 1999). For example, in the former mixed exhibit at Beekse Bergen baboons infected elephants with salmonella. To prevent further cases of cross-species contamination, the animals were separated (Huber and Kaandorp, 2000). Epidemiologically, it has to be considered that mammal species have coevolved with specific pathogens, with consequent development of coping strategies. On the other hand, different species which might never have had contact with one another in the wild do live together in zoos. Hence, infectious agents which might have a different pathogenicity for different species could be transmitted between them. For example, the protozoon *Balantidium coli* is innocuous for all Cercopithecinae, but might cause severe infections in apes, especially in gorillas. Amoebas, which do not normally cause clinical symptoms in New World monkeys, might cause severe problems in Colobidae (Loomis *et al.*, 1983). Herpesviruses are known to cause inapparent infection in their natural host, whereas in other species they can cause severe disease. Examples are *Herpesvirus saimiri* from squirrel monkeys, *H. ateles* from spider monkeys and Medical Lake herpesvirus from macaques (Meinl, 1998). Likewise, it cannot be ruled out that African elephants are the origin of infection for lethal herpesvirus infection in Asiatic elephants. For this reason, nowadays, African and Asiatic elephants are usually kept separately from each other. Concerning viruses associated with malignant catarrhal fever (MCFV), however, as well as bacteria from the genus *Chlamydophila*, it has been estimated that all animals of a zoological collection create an epidemiological unit. Hence, animals within a mixed-species exhibit are not exposed to a higher infection rate than animals in single-species exhibits (Probst *et al.*, 2007).

Discussion

Nowadays, most Central European zoos present their animals in naturalistic exhibits showing different species. The benefits which result from this type of husbandry include the possibility of species-specific behaviour and a better educational experience for the visitor. Nevertheless, the educational advantage cannot be claimed as a convincing argument unless the visitor's interest is further developed by providing information. This could include briefings on such concepts as ecological niche, symbiosis, commensalism, communication, individual flight distance, and strategies for solving social conflicts. On the other hand, mixed-species displays also have disadvantages, especially with regard to breeding success. Some animals do not reproduce successfully, either because the sex ratio does not reflect a normal situation or because the rearing of young is disturbed by the cohabiting species. Birds that live together with mammals often need to have their wings clipped, which may mean that males are unable to keep their balance while copulating with the females and the eggs remain unfertilized. In other cases birds lay fertile eggs, but do not incubate them because of lack of privacy. In what follows, we discuss some factors that should be considered when planning and managing a mixed-species exhibit. The listed factors define the basis of an ecosystem and should not be regarded each for itself, but all collectively.

A. Management

· **Exhibit design.** Exhibit design is a crucial factor for long-term success, as social incompatibility is a frequent problem in mixed-species exhibits (Thomas and Maruska, 1996). The criteria are principally the same for developing a mixed- and a single-species display (exhibit size, visual barriers, hiding areas, etc.). Additionally, peculiarities of different species have to be considered. For example, if hoofed mammals are housed together with burrowing animals, like bison with prairie dogs at Prague Zoo or ibex with marmots at Nuremberg, the ungulates might stumble across the holes on the ground. Also, it is advantageous if the animals can get out of each other's way by an ability the other species does not have, like climbing, flying, digging etc. For example, at Apenheul, the Netherlands, the black spider monkeys have the possibility to jump up into a separate exhibit area, while the cohabiting capybaras can swim across the water to their own little island. In Stralsund Tierpark the corsac foxes could evade the cohabitant Asian lions by retiring into the burrows they had dug for themselves (Hähn, 2003).

· **Staff capacity.** Mixed-species exhibits require a higher level of attention than each species requires when kept on its own. Hence, the keepers should agree to invest more time and patience into monitoring animal behaviour.

· **Introduction procedure.** It may be easier to mix different species in an exhibit which is new for all of them than to introduce a new species to an established exhibit. In the latter case, the 'old' species has to be removed first and the new one must be given the chance to get familiar with the exhibit's routes of escape and places to hide. In this way, none of the species has a 'home field' advantage or a territorial claim. Getting the animals habituated to each other may require a variable amount of time. It might be beneficial to mix high-ranking animals first. Another possibility would be to first allow the animals to become visually and olfactorily acquainted with each other (Thomas and Maruska, 1996). Each species' behaviour should be closely monitored and documented.

· **Feeding regime.** Disputes over food are a frequent cause of aggression and might be relieved either by providing food in dispersed locations throughout the exhibit or by feeding the main portion in the stalls.

· **Public relations.** Involving the visitors in the experiences resulting from mixed-species exhibits makes good sense in any case.

B. Species-specific characteristics

Guidelines of species selection for mixed exhibits are listed in Thomas and Maruska (1996).

· **Body size.** Body size difference might be an important factor in cases of mixing taxonomically-related species, like dama gazelle with gemsbok or lesser kudu with impala (Popp and Bunkfeldt-Popp, 1986). On the other hand, in Halle and Cologne Zoos, Germany, mixing different species of marmosets and tamarins led to a settled dominance hierarchy with low rates of aggression.

· **Nutrition.** If predators are mixed with other species, the advantages should be weighed up carefully against the risk of permanently stressed cohabitants: e.g. leopards with pigeons at Dählhölzli Tierpark, Bern, Switzerland, or red pandas with white eared pheasants in Görlitz Tierpark, Germany. Furthermore, it should be considered that mineral and vitamin needs might vary considerably from species to species (Kenny *et al.*, 1993). An exhibit with mouse lemurs and tenrecs had to be abandoned because the lemurs became so obese from eating tenrec food (Baker, 1992).

· **Ecological niche.** If the species to be combined occupy the same ecological niche *in situ*, the keepers should be alert for (subtle) abnormal behavioural changes (Xanten, 1992). Nevertheless, species occupying the same niche can cohabit quite well together, as for example the mixed-species *Saguinus* groups at Belfast Zoo, Northern Ireland (Hardie *et al.*, 2003), or the titis, marmosets and sloths at Berlin Zoo (Table 1, No. 9; see also photo, p. 333). Hardie *et al.* (2003) even regard the fact of the species being sympatric in the wild as an additional criterion for success. In some exhibits arboreal and terrestrial or aquatic species can be maintained together, like bearded vultures with Arctic hares or siamangs with pacaranas (Table 1, Nos. 54, 62), or armadillos with sloths or with squirrel monkeys.

· **Activity periods.** Animals with opposite day–night rhythms do not compete with each other, allowing an efficient use of space. Furthermore, they give the visitors the opportunity to see an active exhibit at all times. A successful example is nocturnal maned wolves sharing their enclosure with diurnal giant anteaters at Edinburgh Zoo. Nevertheless, it should be kept in mind that the animals might also disturb each other while resting, as could happen with night monkeys and squirrel monkeys.

· **Social compatibility of species.** Mammals possess different levels of social tolerance. Certain species tend to be placid and tolerant, whereas others, including black rhinos and white-tailed gnus, are inherently aggressive towards other species. Hence, these species are almost never mixed with other species. Animals with a large individual distance like musk oxen are also rather unsuitable for mixed exhibits. Therefore, apart from Munich Tierpark Hellabrunn, Germany, where they are mixed with beavers, and Helsinki Zoo, Finland, where they are mixed with Arctic foxes, musk oxen are usually housed in single-species exhibits. Both examples emphasize the importance of backup capacities through specific abilities (swimming, running). Predators are seldom mixed with other species. A rather common exception is the combination brown bears with wolves (Fig. 6). Another remarkable combination can be seen at Nadermann Tierpark, Delbrück, Germany – servals, crab-eating macaques, donkeys, eland and domestic goats.

· **Territoriality and mating activity.** One of the main factors in initiating aggressive interactions is undoubtedly mating activities, more precisely breeding

Common marmoset and titi monkey, Berlin Zoo, 2006. (Photo: Christian Matschei)

males. This problem can be kept within limits by excluding females and mixing bachelor groups. For example, male Thomson's gazelles are highly territorial animals. Therefore they are kept at Leipzig and Hannover Zoos in multi-male groups in mixed exhibits.

· **Natural group composition.** It is impressive that some asocial species can be housed together with other species without much conflict, like red pandas and musk deer. Also species which would not tolerate other conspecific males in the same cage, like different marmosets and tamarins, might accept adult males of other callitrichid species.

· **Threat displays, submission signals, fighting techniques.** Distantly related species might possess very different intimidation patterns and submission signals. For example, some species of deer, sheep, and goats point their head down and forward, while blackbucks lift it up. At first sight zebras and hippos might have similar strategies of threat: both bare their teeth. But hippos do it by yawning, while zebras do it by lifting their lips. Rhinos, however, use their horns to threaten. Addax and bantengs show aggression by digging soil with their horns. Fighting techniques may be very different as well. Mixing ritualized fighters with damage fighters should be avoided (e.g. Alpine ibex with chamois). It should also be noted that some smaller species might inflict serious injuries on larger ones (Puschmann, 2004), as in the case of red river hogs at Duisburg Zoo, Germany, which inflicted serious biting wounds on the legs of cohabitant domestic cattle.

· **Taxonomic relatedness.** Concerning this factor, opposite hypotheses have been developed. One postulates that the rate of aggression is highest among closely-related species (Walther, 1965). Other studies, however, revealed that closely-related species can coexist without major problems (Popp, 1984; Wojciechowski, 2004).

· **Hybridisation/heterospecific copulation.** The possibility of undesirable hybridisation should be kept in mind, e.g. between different waterbuck species, yaks and gayals, or bantengs and zebus. Attempts to copulate or actual copulation has been observed between mhorr gazelles and sand gazelles as well as between saiga antelopes and goitered gazelles. At Krefeld Zoo adult greater kudus do not interfere when their young are mounted by springboks. At Wilhelma Zoologisch-Botanischer Garten, Stuttgart, Germany, gelada baboons copulate with young Barbary sheep (Rietschel, pers. comm.).

Porcupines in the Arche Noah Zoo Braunschweig prefer to graze directly around the resting Bactrian camels. This female loses her patience and snaps at the molester. (Photo: Carolina Probst, November 2007)

C. Individual factors

· **Age and familiarity with other species.** These two factors often decide whether a combination of species is successful or not. Preferably young animals should be chosen, especially in the case of males. Old animals who do not have any experience of cohabiting with other species should be mixed only in exceptional circumstances, as in the case of individual social primates whose conspecifics have passed away or who have been driven out of the group: at Ulm Zoo, Germany, the last surviving female of a large group of vervet monkeys shares her enclosure with a domestic rabbit. Since the integration, the monkey has demonstrated a much higher rate of activity and alertness (Müller, pers. comm.).

· **Individual character.** In most cases, the animals' individual characters are the crucial factor in deciding the success or failure of a mixed-species exhibit (Sodaro and Saunders, 1999).
· **Hand-reared individuals.** It should be kept in mind that introducing hand-reared animals which are focused on humans into a mixed exhibit might be problematical.

D. Special situations

· **Birth and rearing of young.** It must be taken into account that births may trigger aggression in cohabitant species. This problem can be solved by providing enough refuges for the young and by separating mothers with their offspring until they are capable of moving to those refuges. In particular, zebras represent a potential source of danger. The mixed exhibit of waterbucks, Chapman's zebras and ostriches at Tierpark Hagenbeck, Hamburg, Germany, functioned without any problems until a waterbuck was born. The level of harassment of the fawn escalated to the point where it became necessary to separate the waterbucks. Subsequently, they were replaced by wart hogs. These give birth at the end of November, when the exhibit is only occupied for a few hours a day. Therefore, the piglets are not confronted with the zebras until they are half a year old (Kershaw, 2005). In other cases it might be sufficient to separate the animals for a limited length of time. For example, at Halle Zoo squirrel monkeys destroyed a nest of trumpeters. Subsequently, the birds were removed from the exhibit and were reintroduced into the tropical hall with their chicks after breeding successfully.
· **Introduction of new animals.** The procedure for introducing a new animal into a mixed-species exhibit is principally the same as accustoming it to a single-species exhibit. Nevertheless, in addition to the sex, age and reproductive status of the animal, its habituation to the other species also has to be considered. For example, a Bactrian camel at Arche Zoo Braunschweig, Germany, learned by experience that stepping on a porcupine hurts (see photo, p. 334).

E. Animal welfare legislation

Some mixed-species exhibits involve a balancing act between behavioural enrichment and compromising the quality of animal welfare. Is it fair if a finch is eaten by a meerkat or a pigeon by a leopard? If the answer is yes, the visitors should be informed on the arguments and background.

Conclusion

In the wild, different animal species tend to form heterospecific groups in order to improve defence against predators and to optimize access to food. In contrast, the reasons for keeping captive animals in heterospecific groups are different, being based on ethological as well as educational and economic advantages. On the other hand, it may cause stress and provoke severe interspecific conflicts. This paper balances the advantages and disadvantages of several mixed exhibits in Central European zoos. Finally, factors that play a role in the success of mixed-species displays are discussed. Despite considering all factors, one and the same combination of species might be highly successful in one zoo and plagued with difficulties in another. To sum up, though, we believe that properly managed mixed-species exhibits are much more appealing than single-species exhibits. Table 1 lists examples of notable mixed-species exhibits with mammals in Central European zoos, but is by no means complete.

When the wolves at Berlin Zoo have their fast day, they stare at the bear's food. (Photo: Carolina Probst, May 2006)

Table 1. Selected mixed-species exhibits with mammals in Central European zoos (Germany, Austria, Switzerland, Czech Republic).

No.	Ungulates	Carnivores	Primates	Others
1.			Cotton-top tamarin *Saguinus oedipus*	Ringed teal *Calonetta leucophrys*
2.				Humboldt's penguin *Spheniscus humboldti* Mara *Dolichotis patagonum*
3.				Two-toed sloth *Choloepus didactylus* Capybara *Hydrochaeris hydrochaeris*
4.		Badger *Meles meles*		Hooded crow *Corvus c. cornix* Magpie *Pica pica*

No.	Ungulates	Carnivores	Primates	Others
5.		Zebra mongoose *Mungos mungo*		Rhea *Rhea americana*
6.	Okapi *Okapia johnstoni* Red duiker *Cephalophus natalensis*			
7.	Sable antelope *Hippotragus niger* Kirk's dik-dik *Madoqua kirkii*			
8.		Meerkat *Suricata suricatta*		Weaverbird *Ploceus jacksoni*
9.			Common marmoset *Callithrix jacchus* Titi monkey *Callicebus cupreus*	Two-toed sloth *Choloepus didactylus* Agouti *Dasyprocta* sp.
10.	Hippopotamus *Hippopotamus amphibius* Nyala *Tragelaphus angasi*			Egyptian goose *Alopochen aegyptiacus* Marabou *Leptoptilos crumeniferus*
11.		Brown bear *Ursus arctos* Grey wolf *Canis l. lupus*		
12.	White rhinoceros *Ceratotherium s. simum* Dwarf (domestic) goat *Capra hircus*			
13.	Lowland tapir *Tapirus terrestris*			Capybara *Hydrochaeris hydrochaeris* Mara *Dolichotis patagonum*
14.		Arctic fox *Alopex lagopus*		Snowy owl *Nyctea scandiaca*
15.	Hog deer *Axis porcinus* Nilgai *Boselaphus tragocamelus*			

No.	Ungulates	Carnivores	Primates	Others
16.	Vicugna *Lama vicugna*			Capybara *Hydrochaeris hydrochaeris* Mara *Dolichotis patagonum* Rhea *Rhea americana*
17.			Gelada baboon *Therophithecus gelada*	Griffon vulture *Gyps fulvus* Marabou *Leptoptilos crumeniferus*
18.	Giraffe *Giraffa c. rothschildi* Grevy's zebra *Equus grevyi* Scimitar-horned oryx *Oryx dammah* Thomson's gazelle *Gazella thomsonii*			Lesser flamingo *Phoeniconaias minor* Marabou *Leptoptilos crumeniferus* Southern hornbill *Bucorvus cafer* Ostrich *Struthio camelus australis*
19.	Eld's deer *Cervus eldi thamin* Musk deer *Moschus moschiferus*			White-naped crane *Grus vipio* Red-crowned crane *Grus japonensis*
20.		Sloth bear *Melursus ursinus*	Rhesus macaque *Macaca mulatta*	
21.	Kiang *Equus hemionus kiang* Hornless yak *Bos grunniens*			White-eye *Aythya nyroca* Teal *Anas crecca*
22.	Bactrian camel *Camelus bactrianus*			Porcupine *Hystrix leucura*
23.			Saimiri *Saimiri sciureus*	Trumpeter *Psophia crepitans*
24.			Common marmoset *Callithrix jacchus*	Red-backed parrot *Psephotus haematogaster* Acouchi *Myoprocta acouchi*
25.			Red-handed tamarin *Saguinus m. midas*	Three-banded armadillo *Tolypeutes matacus*
26.		Coati *Nasua nasua*	Capuchin *Cebus apella*	

No.	Ungulates	Carnivores	Primates	Others
27.			Golden lion tamarin *Leontophithecus rosalia*	Agouti *Dasyprocta* sp.
28.	Bush hyrax *Heterohyrax brucei*			Ground squirrel *Xerini inauris* Spurred tortoise *Geochelone sulcata*
29.	Banteng *Bos javanicus* Axis deer *Axis axis*			
30.	Muntjac deer *Muntiacus reevesi*	Red panda *Ailurus f. fulgens*		White eared pheasant *Crossoptilon crossoptilon*
31.	Lowland tapir *Tapirus terrestris* Southern pudu *Pudu pudu*			Giant anteater *Myrmecophaga tridactyla* Capybara *Hydrochaeris hydrochaeris* Screamer *Chauna torquata*
32.	Eland *Taurotragus oryx* Greater kudu *Tragelaphus strepsiceros*			Griffon vulture *Gyps fulvus* Marabou *Leptoptilos crumeniferus*
33.	Hartebeest *Alcelaphus buselaphus*			Ostrich *Struthio camelus australis*
34.	Asiatic elephant *Elephas maximus* Blackbuck *Antilope cervicapra* Axis deer *Axis axis*			
35.	Dwarf goat *Capra hircus*	Grey mongoose *Herpestes edwardsi*	Rhesus macaque *Macaca mulatta*	
36.	Blue wildebeest *Connochaetes taurinus* Red duiker *Cephalophus natalensis* Mountain zebra *Equus zebra hartmannae*			Crowned crane *Balearica pavonina* African shelduck *Tadorna cana*

No.	Ungulates	Carnivores	Primates	Others
37.	Banteng *Bos javanicus* Nilgai *Boselaphus tragocamelus*			
38.	Red duiker *Cephalophus natalensis*			Kori bustard *Ardeotis kori*
39.	Barbary sheep *Ammotragus lervia* Rock hyrax *Procavia capensis*		Gelada baboon *Theropithecus gelada*	
40.	Hippopotamus *Hippopotamus amphibius* Grant's zebra *Equus quagga boehmi*			Ostrich *Struthio camelus* ssp.
41.	Red river hog *Potamochoerus porcus*		Sooty mangabey *Cercocebus atys*	
42.				Aardvark *Orycteropus afer* Springhare *Pedetes cafer* Bushbaby *Galago senegalensis*
43.			Owl monkey *Aotes trivirgatus*	Two-toed sloth *Choloepus didactylus*
44.		Lion *Panthera leo* Red meerkat *Cynictis penicillata*		
45.		Small-clawed otter *Amblonyx cinerea*	Orang-utan *Pongo pygmaeus* Lion-tailed macaque *Macaca silenus*	
46.	Nubian ibex *Capra ibex nubiana*		Hamadryas baboon *Papio hamadryas*	
47.	Wood bison *Bison bison athabascae*			Black-tailed prairie dog *Cynomys ludovicianus*
48.	Musk ox *Ovibos m. moschatus*			Canadian beaver *Castor canadensis*
49.	Philippine spotted deer *Cervus alfredi*			Red-crowned crane *Grus japonensis*
50.	Barbary sheep *Ammotragus lervia*		Barbary macaque *Macaca sylvanus*	

No.	Ungulates	Carnivores	Primates	Others
51.	Chamois *Rupicapra rupicapra*	Common otter *Lutra l. lutra*		
52.		Brown bear *Ursus arctos* Lynx *Lynx l. lynx*		
53.	Japanese serow *Capricornis crispus*		Japanese macaque *Macaca fuscata*	
54.				Blue hare *Lepus timidus* Bearded vulture *Gypaetus barbatus*
55.	Pygmy hippopotamus *Choeropsis liberiensis*		Mandrill *Mandrillus sphinx*	
56.			Müller's gibbon *Hylobates muelleri*	Bewick's swan *Cygnus bewickii*
57.			Black gibbon *Nomascus gabriellae* Orang-utan *Pongo pygmaeus*	
58.	Red deer *Cervus elaphus* Mouflon *Ovis ammon musimon*			
59.		Black bear *Ursus americanus* Corsac fox *Alopex corsac*		
60.	Goral *Nemorhaedus goral*			Griffon vulture *Gyps fulvus*
61.	Collared peccary *Tayassu tajacu*	Coati *Nasua nasua*		
62.			Siamang *Symphalangus syndactylus*	Pacarana *Dinomys branickii*
63.	Giraffe *Giraffa c. reticulata* Thomson's gazelle *Gazella thomsonii*			

No.	Ungulates	Carnivores	Primates	Others
64.			Mandrill *Mandrillus sphinx* Vervet monkey *Cercopithecus aethiops*	

Comments on Table 1

1. Bernburg Zoo. No problems reported (2007).
2. Eberswalde Zoo. Penguins had health problems after stealing mouldy hay from the maras.
3. Chemnitz Tierpark. During winter 1.0 sloth together with 2.2 capybaras. No problems reported (2007).
4. Gera Tierpark. One badger with birds. No problems reported (2007). [In Bremerhaven Zoo, one badger with fox in a small exhibit, no problems either, species ignore each other (2006).]
5. Stassfurt Zoo. Two rheas and seven mongooses; no problems reported (2007).
6. Berlin Zoo, Leipzig Zoo. Successful.
7. Basel Zoo (Switzerland), Berlin Zoo. Successful; backup possibilities for dik-diks are necessary.
8. Berlin Zoo. Successful, but birds may be caught by meerkats (2007)
9. Berlin Zoo. Primates with two sloths and individuals of other species successful (2007).
10. Berlin Zoo. Successful; hippos interact with nyalas; sufficient backup possibilities are necessary.
11. Schwerin Zoo, Berlin Zoo, Eberswalde Zoo, Johannismühle Wildpark, Lüneburger Heide Wildpark, Bernburg Zoo. Successful; wolf cubs are in danger. At Schwerin Zoo wolves were killed by bears (Zessin, 2006).
12. Schwerin Zoo. Unique combination in Germany; successful (Zscheile, 1999).
13. Schwerin Zoo. No problems reported; all species breed regularly.
14. Dresden Zoo. Two owls and two foxes; only possible with adult specimens (2007). In Bremerhaven Zoo am Meer 1.2 Arctic foxes with 2.0 snowy owls (2006).
15. Dresden Zoo. Successful (2007).
16. Munich Tierpark Hellabrunn, Dresden Zoo, Halle Zoo. Successful; at Halle Zoo with 1.2 rheas (*Pterocnemia pennata*) (2007), at Berlin Zoo, instead of vicugnas, guanacos and 1.0 red brocket.
17. Dresden Zoo. Successful, lots of interactions between 2.0 baboons and the marabou, which is dominant (2007).
18. Leipzig Zoo, Magdeburg Zoo. Successful; at Leipzig, problems between hornbills and cranes (2007).
19. Leipzig Zoo. Successful; musk deer in both crane groups; musk deer with deer.
20. Leipzig Zoo. Successful; bears tolerate monkeys riding on their backs (2007).
21. Berlin Tierpark. Kiangs attack yak calves. Kiangs and yaks need to have separate feeding places (2007).
22. Braunschweig Arche Noah Zoo. Successful; only an inexperienced camel stepped on a porcupine (Blankenburg, pers. comm.).
23. Halle Zoo. Successful; approx. 50 monkeys and three trumpeters with chicks

in tropical hall (2007).

24. Rostock Zoo. No problems reported.
25. Rostock Zoo, Halle Zoo. No problems reported; at Rostock Zoo 1.0 large hairy armadillo (2007); at Berlin Tierpark mixed exhibit was abandoned because of losses among the young tamarins (2005).
26. Rostock Zoo. Successful.
27. Magdeburg Zoo. Successful.
28. Cottbus Tierpark. Successful; both species breed regularly basis (2007).
29. Cottbus Tierpark: successful; both species (1.2 bantengs; 11 deer) breed regularly (2007).
30. Görlitz Tierpark, Berlin Zoo, Nuremberg Zoo, Hannover Zoo. Mostly successful; pandas killed muntjac calves at Görlitz and Nuremberg. At Krefeld Zoo there were losses among panda cubs as well as muntjac (*Muntiacus reevesi micrurus*) calves.
31. Dortmund Zoo. Successful; interactions between tapirs and anteaters (Bartmann, 1980, Seitz, 2001).
32. Gelsenkirchen Zoom Erlebniswelt. Successful; vulture picks at eland hair (Gürtler, 2001).
33. Hannover Zoo. Successful (2006).
34. Heidelberg Zoo. Successful; deer can retire into a separate area protected by electric fence.
35. Heidelberg Zoo. Successful; monkeys and goats eat together.
36. Landau Zoo. Successful; positive interactions between all species (Honigs *et al.*, 2006).
37. Nuremberg Zoo. Mixed exhibit was abandoned because of interspecific conflicts between males (Mägdefrau, 2002).
38. Nuremberg Zoo. Successful; 1.1 duikers eat from the bustards' minced meat.
39. Wilhelma Zoo, Stuttgart. Geladas ride on sheep and milk them; low-ranking monkeys copulate with lambs (Rietschel, pers. comm.); similar mixtures in Rheine Naturzoo and Schloss Herberstein Tier- und Naturpark (Austria).
40. Basel Zoo. Long-term successful with one exception: zebra stallion was killed by hippos.
41. Salzburg Zoo (Austria). Successful; mangabeys (*Cercocebus atys lunulatus*) ride on pigs.
42. Berlin Zoo. Successful (2007).
43. Dortmund Zoo. Successful (2006).
44. Schwerin Zoo. Lions killed mongooses. At Stralsund Tierpark successful combination of lions (*P. l. persica*) and corsacs for five years; the last remaining corsac was probably killed by female lion. At present combination of corsacs and bears (*U. a. syriacus*). At Mühlenhagen Naturerlebnispark successful combination of corsacs and domestic goats.
45. Münster Zoo, Hagenbeck Tierpark. Successful; in Hamburg without *M. silenus*.
46. Munich Tierpark Hellabrunn. Existed until 2007 (3.0 ibex died).
47. Munich Tierpark Hellabrunn. Unintentional, but successful; prairie dogs collect hair from bison.
48. Munich Tierpark Hellabrunn. Musk oxen killed beavers; at Helsinki Zoo successful combination of musk oxen and Arctic foxes (*Alopex lagopus*).
49. Schönbrunn Zoo, Vienna (Austria). Successful (2007).
50. Schönbrunn Zoo, Vienna (Austria). Successful; species interact with each other and breed regularly.

51. Salzburg Zoo (Austria). Successful (2006).
52. Salzburg Zoo. Works only if enough backup possibilities for lynxes.
53. Schönbrunn Zoo, Vienna (Austria). Not successful; at present successful combination of serows with domestic chickens (2007); serows breed regularly.
54. Schönbrunn Zoo, Vienna (Austria), Goldau Tierpark (Switzerland). Sufficient backup possibilities for hares are necessary; combination was abandoned in Vienna (2007).
55. Halle Zoo. Mangabeys bothered 1.1 pygmy hippos, so mixed exhibit with mangabeys was abandoned; at present hippos with various callitrichid species (c. ten *Saguinus midas*, c. five *Saguinus fuscicollis*, c. six *Callinico goeldii*) (2007).
56. Cottbus Tierpark. Successful (2007).
57. Leipzig Zoo. Successful; interactions between 0.1 gibbon and orangutans (2007).
58. Berlin Tierpark, Dortmund Zoo, several wild animal parks. Mostly successful; in Berlin several male mouflons were killed by male deer, so mixed exhibit was abandoned .
59. Stralsund Tierpark. New combination, until now no complications reported (2007).
60. Plzen Zoo (Czech Republic). Successful (2003). At Nordhorn Tierpark (Germany) successful combination of ibex (*Capra ibex sibirica*) and griffon vultures.
61. Liberec Zoo (Czech Republic). Successful (2007).
62. Berlin Zoo. Successful (2006).
63. Frankfurt/Main Zoo. Male gazelle attacked and hurt giraffes, so mixed exhibit was abandoned; at Hannover Zoo successful combination of giraffes and springboks (*Antidorcas marsupialis*) (2006).
64. Schloss Herberstein Tier- und Naturpark (Austria). Successful.

References

Backhaus, D., and Frädrich, H. (1965): Experiences keeping various species of ungulates together at Frankfurt Zoo. *Int. Zoo Yearbook* 5: 14–24.

Baker, B. (1992): Guess who's coming to dinner: an overview of mixed species primate exhibits. *AAZPA Regional Conference Proceedings*: 62–67.

Bartmann, W. (1980): Keeping and breeding a mixed group of large South American mammals at Dortmund Zoo. *Int. Zoo Yearbook* 20: 271–274.

Bearzi, M. (2005): California sea lions use dolphins to locate food. *J. Mammal.* 87 (3): 606–617.

Berggren, S. (1969): *Mein Tierparadies*. Rowohlt Verlag, Reinbek.

Boinski, S., and Garber, P.A. (2000): *On the Move: How and Why Animals Travel in Groups*. University of Chicago Press, Chicago.

Burkhardt, C. (2006): Intra- und interspezifische Verhaltensweisen von Orang-Utan (*Pongo pygmaeus abelii*) und Schabrackentapir (*Tapirus indicus*) in Menschenhand: Prognosen zur Gemeinschaftshaltung. *Zool. Garten* N.F. 75 (5–6): 317–329.

Crotty, M.J. (1981): Mixed species exhibits at the Los Angeles Zoo. *Int. Zoo Yearbook* 21: 203–206.

Damen, M. (2007): Zwei Tierarten auf einem Kissen, liegt der Teufel dann dazwischen? Presentation, Zookunft, Magdeburg, February 2007.

Deegener, P. (1918): *Die Formen der Vergesellschaftung im Tierreiche*. Verlag von Veit and Comp., Leipzig.

Deleu, R., Veenhuizen, R., and Nelissen, M. (2003): Evaluation of the mixed-species exhibit of African elephants and hamadryas baboons in Safari Beekse Bergen, the

Netherlands. *Primate Report* 65: 5–19.
Dickman, C.R. (1992): Commensal and mutualistic interactions among terrestrial vertebrates. *Trends Ecol. Evol.* 7: 194–197.
Dittrich, L. (1968): Erfahrungen bei der Gesellschaftshaltung verschiedener Huftierarten. *Zool. Garten* N.F. 36: 95–106.
Elder, W.H., and Elder, N.L. (1970): Social groupings and primate associations of the bushbucks (*Tragelaphus scriptus*): *Mammalia* 34: 356–362.
Encke, W. (1997): Afrikanische Antilopen im Krefelder Zoo. *Zoo Magazin* 2: 12–14.
Fitzgibbon, C.D. (1990): Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Anim. Behav.* 39: 1116–1126.
Forthman, D.L., McManamon, R., Levi, U.A., and Bruner, G.Y. (1995): Interdisciplinary issues in the design of mammal exhibits. In *Conservation of Endangered Species in Captivity* (eds. E.F. Gibbons, Jr., B.S. Durrant and J. Demarest), 377–399. State University of New York, Albany.
Giraldeau, L.A. (1984): Group foraging: the skill pool effect and frequency-dependent learning. *Am. Nat.* 124 (1): 72–79.
Gürtler, W.-D. (2001): Ungewöhnliche Tierpartnerschaften. *Zoo Magazin NRW* 3: 52–57.
Hammer, G. (2002): Gemeinschaftshaltungen von Säugetieren in Zoos: Bestandserhebung und Problematik. Vet. Med. Dissertation, Naturwissenschaftlichen Fakultät der Universität Salzburg.
Hähn, K. (2003): Verhaltensstudie zum Zeitbudget von Korsakfüchsen (*Vulpes corsac*) in Nachbarschaft zu Indischen Löwen (*Panthera leo persica*) am Beispiel eines Gemeinschaftsgeheges im Tierpark Stralsund. Diplomate Thesis, Ernst-Moritz-Arndt-Universität Greifswald.
Hänichen, T., Reid, H.W., Wiesner, H., and Hermanns, W. (1998): Bösartiges Katarrhalfieber bei Zoowiederkäuern. *Tierärztl. Prax.* 26: 294–300.
Hardie, S.M., Prescott, M.J., and Buchanan-Smith, H.M. (2003): Ten years of tamarin mixed-species troops at Belfast Zoological Gardens. *Primate Report* 65: 21–38.
Hodge, M.A., and Uetz, G.W. (1992): Antipredator benefits of single- and mixed-species grouping by *Nephila clavipes* (L.): *J. of Arachnology* 20 (3): 212–216.
Honer, O.P., Leumann, L., and Noe, R. (1997): Dyadic associations of red colobus and Diana monkey groups in the Taï National Park, Ivory Coast. *Primates* 38 (3): 281–291.
Honigs, S., Heckel, J.-O., and Buchert, P. (2006): Neue Anlage für afrikanische Huftiere im Zoo Landau in der Pfalz. *TR* 1: 10–14.
Huber, C., and Kaandorp, J. (2000): *Salmonella typhimurium* in einem gemischten Gehege aus Mantelpavianen (*Papio hamadryas*) und afrikanischen Elefanten (*Loxodonta africana*). Presentation, 20. Arbeitstagung der Zootierärzte im deutschsprachigen Raum, Salzburg, Austria, November 2000.
Itzkowitz, M. (1977): Social dynamics of mixed-species groups of Jamaican reef fishes. *Behav. Ecol. Sociobiol.* 2: 361–384.
Kenny, D., Cambre, R.C., Lewandowski, A., Pelto, J.A., Irlbeck, N.A., Wilson, H., Mierau, G.W., Sill, F.G., and Garcia, A.P. (1993): Suspected vitamin D_3 toxicity in pacas (*Cuniculus paca*) and agoutis (*Dasyprocta aguti*). *J. Zoo Wildl. Med.* 24: 129–139.
Kershaw, T. (2005): Vergesellschaftung von Warzenschweinen, Zebras und Straussen. *Arbeitsplatz Zoo* 3: 8–9.
Kratochwil, A., and Schwabe, A. (2001): *Ökologie der Lebensgemeinschaften*. Ulmer Verlag.
Krebs, J.R., and Davies, N.B. (1997): An Introduction to Behavioural Ecology. Blackwell Scientific Publications, Oxford.
Landeau, L., and Terborgh, J. (1986): Oddity and the 'confusion effect' in predation. *Animal Behaviour* 34: 1372–1380.
Linnenberg, M. (1994): Untersuchungen zum intra- und interspezifischen Verhalten von Boviden und Equiden im Zoo. Diploma thesis, Institut für Zoologie der Tierärztlichen Hochschule Hannover.
Loomis, M.R., Britt, J.O., Gendron, A.P., Holshuh, H.J., and Howard, E.B. (1983): Hepatic and gastric amebiasis in black and white colobus monkeys. *J. Am. Vet. Med. Assoc.* 183: 1188–1191.

Lowenstine, L. (1999): Health problems in mixed-species exhibits. In *Zoo and Wild Animal Medicine: Current Therapy 4* (eds. M. Fowler and R. Miller), pp. 26–29. WB Saunders Co., Philadelphia.

Mägdefrau, H. (2002): Neben-, Gegen- oder Miteinander. *Manati* (Magazin des Vereins der Tiergartenfreunde Nürnberg e.V.) 1: 10–12.

Majolo, B., and Ventura, R. (2004): Apparent feeding association between Japanese macaques (*Macaca fuscata yakui*) and sika deer (*Cervus nippon*) living on Yakushima Island, Japan. *Ethol. Ecol. Evol.* 16: 33–40.

Mathis, A., and Chivers, D.P. (2003): Overriding the oddity effect in mixed-species aggregations: group choice by armoured and nonarmoured prey. *Beh. Ecol.* 14 (3): 334–339.

McAloose, D. (2004): Health issues in naturalistic mixed-species environments: a day of a zoo pathologist. 55th Annual Meeting of the ACVP and 39th Annual Meeting of the ASVCP.

Meinl, E. (1998): Zur Biologie von Herpesviren beim Menschen und nichtmenschlichen Primaten. Deutsches Primatenzentrum Symposium, 03.12.1998.

Morse, D.H. (1977): Feeding behaviour and predator avoidance in heterospecific groups. *BioScience* 27 (5): 332–339.

Nobert, B. (2001): Das Erweiterungsgelände im Zoo Berlin. *Zoo Magazin Nord-Ost* 1: 80–83.

Noë, R., and Bshary, R. (1997): The formation of red colobus – diana monkey associations under predation pressure from chimpanzees. *Proc. Roy. Soc. Lond.* 264: 253–259.

Oberwemmer, F. (2004): Afrika-Flair im Zoo Leipzig. *TR* 2/04: 23–28.

Peres, C.A. (1993): Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatol.* 61: 61–76.

Popp, J.W. (1984): Interspecific aggression in mixed ungulate species exhibits. *Zoo Biology* 3: 211–219.

Popp, J.W., and Bunkfeldt-Popp, L. (1986): Interspecific aggression among female ungulates. *Aggressive Behaviour* 12: 197–200.

Probst, C., Speck, S., and Hofer, H. (2007): Epidemiology of selected infectious diseases in zoo ungulates: single species versus mixed species exhibits. *Int. Symp. Erkr. Zootiere* 7: 10–12.

Puschmann, W. (ed.) (2004): *Zootierhaltung: Tiere in menschlicher Obhut. Säugetiere.* Verlag Harry Deutsch, Frankfurt am Main.

Rasa, O.A.E. (1983): Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. *Beh. Ecol. Sociobiol.* 12: 181–190.

Ruggiero, R.G., and Eves, H.E. (1998): Bird–mammal association in forest openings of northern Congo (Brazzaville). *African J. of Ecology* 36 (2): 183–193.

Sazima, I., Sazima, C., and Da Silva, J.M. (2006): Fishes associated with spinner dolphins at Fernando de Noronha Archipelago, tropical Western Atlantic: an update and overview. *Neotr. Ichth.* 4 (4): 451–455.

Schaefer, M. (1992): *Ökologie*. (Reihe Wörterbücher der Biologie 3). Gustav Fischer, Stuttgart.

Seitz, S. (2001): Vergleichende Untersuchungen zu Verhalten und Schauwert von Tapiren (Tapiridae) in Zoologischen Gärten. Biologische Dissertation, Ruprecht-Karls-Universität Heidelberg.

Sinclair, A.R.E. (1985): Does interspecific competition or predation shape the African ungulate community? *J. Animal Ecology* 54: 899–918.

Smith, P., and Tucker, M. (1999): Social behavior and interaction of blue monkeys and jackals in a mixed species exhibit. Primate Mixed Species Exhibit Symposium, February 27, Dallas Zoo: 40–44.

Smith, A. A., Kelez, S., and Buchanan-Smith, H.M. (2004): Factors affecting vigilance within wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*). *Behav. Ecol. Sociobiol.* 56: 18–25.

Sodaro, V., and Saunders, N. (1999): Housing and exhibiting mixed species of neotropical primates. Primate Mixed Species Exhibit Symposium, February 27, Dallas Zoo: 53–104.

Stensland, E., Angerbjörn, A., and Berggren, P. (2003): Mixed species groups in mammals. *Mammal Rev.* 33 (3): 205–223.
Taylor, W.A, and Skinner, J.D. (2000): Associative feeding between aardwolves (*Proteles cristatus*) and aardvarks (*Orycteropus afer*). *Mammal Rev.* 30 (2): 141–143.
Thomas, W.D., and Maruska, E.J. (1996): Mixed-species exhibits with mammals. In *Wild Mammals in Captivity – Principles and Techniques* (eds. D.G. Kleiman, M.E. Allen, K.V. Thompson and S. Lumpkin), pp. 204–211. University of Chicago Press, Chicago.
Walther, F. (1965): Ethological aspects of keeping different species of ungulates together in captivity. *Int. Zoo Yearbook* 5: 1–13.
Waser, P.M. (1987): Interactions among primate species. In *Primate Societies* (eds. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker), pp. 210–226. University of Chicago Press, Chicago.
Waser, P.M. (1984): 'Chance' and mixed-species associations. *Beh. Ecol. and Sociobiol.* 15: 197–202.
Waterman, J.M., and Roth, J.D. (2007): Interspecific associations of Cape ground squirrels with two mongoose species: benefit or cost? *Behav. Ecol. Sociobiol.* 61: 1675–1683.
Weidel, A. (2001): Inter- und intraspezifische Unterschiede im Wachsamkeitsverhalten afrikanischer Schleichkatzen. Diplomarbeit, Christian-Albrechts-Universität Kiel.
Wojciechowski, S. (2004): Introducing a fourth primate species to an established mixed-species exhibit of African monkeys. *Zoo Biology* 23: 95–108.
Xanten, W.A. (1992): Mixed species exhibits: are they worth it? *AAZPA Regional Conference Proceedings*: 59–61.
Zessin, W. (2006): Bären und Wölfe im Zoo Schwerin. *TR* 2: 17–20.
Ziegler, T. (2002): Selected mixed species exhibits of primates in German zoological gardens. *Primate Report* 64. Goltze, Göttingen.
Zscheile, K. (1999): Reflexionen einer Vergesellschaftung von Breitmaulnashörnern (*Ceratotherium s. simum*) und Afrikanischen Zwergziegen (*Capra aegagrus f. hircus*) im Schweriner Zoo. *Mitteilungsblatt des Zoovereins Schwerin* 1: 74–76.

Dr. med. vet. Carolina Probst, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany; Dr. rer. nat. Christian Matschei, Peter-Lenné-Schule, special field of zoo animal husbandry, Berlin, Germany. [Correspondence to: Dr C. Probst, Friedrich-Loeffler-Institut, Institute for Epidemiology, Seestrasse 55, 16868 Wusterhausen, Germany (*Tel.*: +49 (0) 33979 80 127; *Fax*: +49 (0) 33979 80 200; *E-mail*: **Carolina.Probst@fli.bund.de**).]

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