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ScienceDirect
APPLIED ANIMAL BEHAVIOUR SCIENCE
Applied Animal Behaviour Science 109 (2008) 105–127
www.elsevier.com/locate/applanim

Review

A preliminary model of human–animal relationships in the zoo

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Accepted 19 April 2007
Available online 21 May 2007

Abstract

The concept of the human–animal relationship (HAR) is widely used in farm animal research to describe the outcome of the different qualities and quantities of interaction between stockpersons and the animals in their care. Thus, negative, positive or neutral HARs may result from the effect of mostly negative (e.g. rough handling), neutral (e.g. no handling) or positive (e.g. gentle handling) interactions. In this paper the concept is applied to zoo animals in an attempt to provide a model not only of HARs between zoo animals and keepers, but also between zoo animals and unfamiliar people, primarily the visiting public. Behavioural responses of animals to zoo visitors are inconsistent both within and between taxa, and the history of interactions the individual animal has experienced, and hence the HARs it has developed, may be one of the variables that leads to this inconsistency. The model starts, like the farm animal models, with the animals' fear of humans, which is itself dependent upon species. The subsequent history of interactions the animal experiences, both with familiar and unfamiliar people, then determines the animal's HAR, which in turn influences the way the animal responds to people. There are currently insufficient data to test the model, but predictions of the model are identified here which could be used to test it.

Keywords: Keepers; Visitors; Interactions; Human–animal relationships

Contents

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doi:10.1016/j.applanim.2007.04.013

1. Introduction

Human and non-human animals come into contact with each other in a variety of settings, and wherever there is contact there is the opportunity for interaction to take place. We are familiar with the interaction that we have with our companion animals, but human–animal interaction also occurs in the context of farms (Hemsworth and Gonyou, 1997; Hemsworth, 2003), laboratories (Chang and Hart, 2002), zoos (Kreger and Mench, 1995) and even the wild (e.g. Cassini, 2001). Repeated interactions between the same animals and humans can lead to the development of a longer-term relationship between the two (Hemsworth et al., 1993). Such relationships have been the subject of considerable research in those contexts where they involve domesticated species. There has been much less research on human–animal relationships involving exotic species, although they have been reported in animals as diverse as wolves (Fentress, 1992), black bears (Burghardt, 1992) and rodents (Dewsbury, 1992). Indeed they have been a necessary aspect of some research projects involving animal–human communication in chimpanzees (Boysen, 1992) and an African grey parrot (Pepperberg, 1992). The aim of this paper is to evaluate how successfully the concept of the human–animal relationship can be applied in the case of zoo animals, and to suggest a model which may have predictive value in helping us to interpret the ways in which zoo animals respond to the people they encounter.

The starting point for relationships to develop is the inter-individual interaction. The term "interaction" can be used in a number of ways; in the classic definition by Hinde (1976) an interaction is usually taken to mean "a sequence in which individual A shows behaviour *X* to individual B, or A shows *X* to B and B responds with *Y*". This is the sense in which I use the term here; it has the advantage that it focuses on the behaviour of the initiator of the interaction, thus allowing us to observe it. It also recognises that an interaction may take place even if there is no observable response by the recipient, and is therefore slightly different from, but in the zoo setting perhaps more useful than, those definitions that stress the behavioural response of the recipient.

A relationship involves "a series of interactions in time" (Hinde, 1976). Hinde, of course, was referring to inter-personal relationships in people, but the notion of a relationship being built up from successive interactions can be applied equally well inter-specifically. Thus, we arrive at the concept of the human–animal relationship (HAR); effectively the human and the animal have a history of interactions between them, and this allows each to make predictions about the behaviour of the other (see Estep and Hetts, 1992). We would expect the development of a HAR to be contingent upon each party being able to recognise the other as an individual, but in principle there is no reason why broader HARs between one person and several animals, or vice versa, may occur if the properties of one partner's behaviour are generalised to other individuals by the other partner (Waiblinger et al., 2006).

Interactions can be perceived by the interacters as negative, neutral or positive (Waiblinger et al., 2006), and the ultimate effect of these will be to bring about a predominantly negative, neutral or positive HAR. How interactions are perceived is affected not only by the nature of the interaction itself, but also by other variables (Waiblinger et al., 2006) such as the past experience of the individual of other interactions, the interactor's species, personality, motivational state, and no doubt numerous other variables as well. There is now much evidence to indicate that the way the animal perceives interactions, and thus the quality of a particular HAR, can have profound consequences for other aspects of the animal's life.

2. HAR in farmed animals

There has been extensive research on the effects of qualitatively different stockmanship on the behaviour and welfare of farmed animals, notably pigs, sheep, cattle and poultry. Much of this research has been reviewed recently (Hemsworth, 2003; Boivin et al., 2003; Waiblinger et al., 2006) and several authors have considered the consequences of stockmanship in terms of the establishment of a HAR. The starting point is the basic fear of the animal towards humans (Hemsworth, 2003); this fear can be reduced if the animal receives positive interactions, such as petting, talking to them and gentle handling, whereas negative interactions, such as hitting, slapping, shouting and rough handling, generally serve to increase the fear of the animal. Increased fear has detrimental effects on the welfare of the animals (Boivin et al., 2003), as well as affecting their behaviour (making them more difficult to handle) and their productivity (Hemsworth, 2003). A reduction in productivity has been linked in these animals to elevated cortisol, implying a long-term stress response (Hemsworth, 2003); some studies, however, while finding behavioural changes in response to humans after rough compared with gentle handling, have not found a link with elevated cortisol or evidence that the animals were experiencing long-term stress (Paterson and Pearce, 1992). The quality of the stockperson's interactions with the animals is very much influenced by their personality and attitudes towards the animals, and the resulting behaviour of the animals can feed back to reinforce or to modify those attitudes (Hemsworth, 2003).

The consequence is that relationships of different quality are set up between the stockperson and their animals. These can be characterised as negative HAR, where the animal has high fear of humans and shows tendencies to avoid contact; neutral HAR, where the animal has low fear of humans, but avoids contact; and positive HAR, where the animal has low fear and shows some confidence with people (Waiblinger et al., 2006). It needs to be pointed out that these relationships are the result of a history of interactions which might contain a mixture of positive, negative and neutral interactions. A positive HAR, based on mostly positive interactions, can still develop even if there are some negative interactions in the history of the relationship (Waiblinger et al., 2006). Thus, the relative quantities as well as the qualities of the different interactions are important in determining the relationship.

3. HAR in laboratory animals

Of course, farm animals have been subjected to a process of domestication favouring reduced anti-predator responses to man and low aggression to man (Fraser and Broom, 1990). Nevertheless there is increasing evidence from laboratory studies that the general principles that are features of the HAR in farmed animals may be true for exotic species in captivity as well. Although there are few empirical studies of the HAR in the laboratory setting, it is widely acknowledged that such relationships exist between laboratory animals and their caretakers (Bayne, 2002; Chang and Hart, 2002).

Laboratory rats can be trained in a conventional test chamber to press a lever where the only reward is social interaction with a human (Davis and Pérusse, 1988), suggesting that the rats were gaining something from the relationship with people. Waitt et al. (2002) showed that there were significantly higher levels of feeding and affiliation in laboratory stump-tailed macaques (*Macaca arctoides*) which had been rated as friendly by their keepers, and higher levels of self-directed and agonistic behaviours in those rated unfriendly, during periods of greater caretaker activity. Although this research concentrated on behavioural correlates of the caretaker's ratings of the animals, and the origin of the unfriendly behaviour could not be conclusively demonstrated, it was still possible to conclude that the quality of the primate-caretaker relationship had important consequences for the behaviour of the animals, and could impact upon welfare. Similarly, Baker (2004) showed that providing laboratory-housed chimpanzees (*Pan troglodytes*) with an additional 10 min per day of contact with a familiar caretaker resulted in the animals showing lower levels of inactivity, some abnormal behaviours, and reactivity to the displays of neighbouring groups compared to the baseline condition. In a different chimpanzee colony, however, the routine presence and activities of caretakers, researchers and veterinary staff during weekdays was correlated with an increased frequency of wounding among the animals (Lambeth et al., 1997). Many routine laboratory procedures are potentially stressful to the animals, and positive reinforcement training is increasingly being used as a way of reducing this stress, and thus improving the welfare of the animals (Schapiro et al., 2003; Laule et al., 2003; Scott et al., 2003). These techniques appear also to improve the relationship between the animals and their caretakers (McKinley et al., 2003; Bassett et al., 2003), presumably because of the reduction of stress, but also because of the amount of time the trainers spend with the animals (Bayne, 2002).

4. Applying the HAR concept to zoo animals

The literature on caretaker–animal relationships in laboratory-housed exotic animals is sparse, and despite some early discussion as to whether positive relationships between humans and laboratory animals could become so positive that they could be regarded as bonds (Davis and Balfour, 1992), the extensive application to exotic animals of the HAR concept used in farm animal research has not really been seen so far. There is in fact no particular reason why we cannot conceive of HARs developing between exotic animals and their keepers, not only in laboratories but also in zoos. An important difference, however, between the zoo environment and the laboratory and farm is the daily presence of large numbers of zoo visitors, and it would be surprising if the quality of animal interactions with zoo visitors were not influenced, and in turn had an influence upon, the relationship that the animals have with their keepers. Thus, in applying the HAR concept to the zoo setting, we need to consider human–animal interactions involving familiar (keepers, other zoo personnel, zoo researchers) and also unfamiliar (zoo visitors) humans.

4.1. Familiar humans

Heini Hediger, who wrote extensively about the different aspects of the zoo environment, and who can probably be regarded as the founder of modern zoo biology, suggested that, of the various ways in which humans might be perceived by zoo animals, keepers were likely to be seen as conspecifics. This could lead to two possible risks: ''the animal sees the keeper as a rival of the same sex and this leads to aggressive behaviour, or it sees in him a potential mate and this may present a danger to the keeper owing to importunate attempts to mate with him'' (Hediger, 1970, p.83). These views, based on many years' experience, were nevertheless made within the ethological framework of the time, and now, forty years on, we can conceive of relationships between animal and keeper that do not have to be based on dominance or imprinting. The important point, however, is that zoo animals probably see the keepers in a different way from the way they see the public (the latter as an enemy, in Hediger's system). For our purposes here, we could re-frame this view in terms of the likelihood that animals in zoos will develop a HAR with their keepers, but may have a different, and probably generalised, relationship with the visiting public.

Few systematic studies have been undertaken on animal–keeper interactions, so evidence for the HAR in zoo animals is sparse. A study by Thompson (1989) of 12 different ungulate species showed that the animals displayed more vigilance towards keepers when the keepers were *in* rather than in front of the enclosure, and they showed more vigilance towards keepers when the public were not present. When the zoo was closed to the public, females, but not males, of large species showed more vigilance towards keepers than small-bodied species. Although superficially this resembles an anti-predator response (i.e. the animals viewed public and keepers as potential predators), Thompson felt that this interpretation was not fully consistent with the data, and that curiosity and monitoring to maintain social cohesion was a better explanation of the changes in behaviour.

Responses of golden-bellied mangabeys (*Cercocebus galeritus chrysogaster*) to both familiar and unfamiliar people at Sacramento Zoo were studied by Mitchell et al. (1991a). These animals threaten people, other monkeys and even inanimate objects. Mitchell et al. (1991a) found that most threats were directed at human visitors, with keepers and observers (i.e. the experimenters) receiving far less threats. It is possible that the animals behaved in this way simply because the visitors and the keepers were behaving towards them in different ways. Nevertheless these authors concluded that zoo visitors were treated like interlopers, keepers like familiar conspecifics, and observers like familiar neighbours. Other primates also behave differently to different categories of humans. Colobus monkeys (*Colobus guereza*) at Paignton Zoo, for example, show different frequencies of interaction with keepers, zoo staff (anyone wearing a zoo uniform but not involved in day-to-day care of those animals) and zoo visitors (Melfi and Thomas, 2005). Interestingly, interactions with all three categories reduced significantly (interactions with zoo visitors stopped altogether) after positive reinforcement training of the animals to facilitate oral examination.

Studies like these indicate that animals as different as primates and ungulates behave differently towards familiar and unfamiliar humans, but do not necessarily provide evidence that HARs have been set up. Some support for the hypothesis that zoo animals establish HARs with their keepers comes from studies on small felids. Mellen (1991), investigating the factors that were associated with reproductive success in small cats, found that, amongst other things, the quality of keeper interactions with the cats was a significant predictor of the cats' reproductive success. In particular, a husbandry style characterised by keepers talking to the cats, and interacting with them, was more likely to be associated with the cats having offspring than a style which did not include such interaction. As a consequence, Mellen (1991) recommended that positive human–animal relationships were desirable for successful reproduction, and that this should start with a socialization process involving, for example, stroking and playing with kittens, the aim being to produce cats with a reduced fear of humans but an enriched environment to facilitate normal behavioural development. In clouded leopards (*Neofelis nebulosa*) faecal corticoid levels were associated negatively with the amount of time primary caretakers spent with the animals, but positively with the number of keepers (Wielebnowski et al., 2002). This was interpreted as indicating that a higher number of keepers probably meant that a predictable, high quality relationship between keeper and cat could not be set up, because individual keepers spent less time with the animals.

Finally, in white rhinoceros (*Ceratotherium simum*), animals which keepers had rated highly in terms of "friendliness to keeper" had significantly lower mean levels of faecal corticoids (Carlstead and Brown, 2005). Although not directly giving evidence of a HAR in these animals, this is nevertheless consistent with the hypothesis that a positive relationship with the caretaker has beneficial effects on the animal's welfare.

4.2. Unfamiliar humans

A number of studies have shown results which are best interpreted as indicating that the presence, and particularly the behaviour, of unfamiliar people (usually zoo visitors) is stressful to zoo animals. For example Chamove et al. (1988) recorded increases in agonistic behaviour and decreases in inactivity and grooming in three different primate species (ringtailed lemur *Lemur catta*, cotton-topped tamarin *Saguinus oedipus* and diana monkey *Cercopithecus diana*) at Edinburgh Zoo when members of the public were present; the changes in behaviour were much less when the visitors were asked to crouch rather than stand in front of the cages. Similarly Mitchell et al. (1991b) found that intra-group aggression doubled when a group of golden-bellied mangabeys was transferred from a cage with low visitor attendance (because of its location within the zoo) to a cage with higher visitor attendance. Most studies have used behavioural measures, but several have used physiological measures. Davis et al. (2005), for example, found that urinary cortisol levels in spider monkeys (*Ateles geoffroyii rufiventris*) at Chester Zoo correlated positively with the number of visitors to the zoo. Similarly, in black rhinoceros higher mean faecal corticoid levels were found in zoos where the animals were kept in enclosures with a greater degree of public exposure (Carlstead and Brown, 2005).

Hosey (2000) reviewed the relevant literature on the responses of zoo animals to human audiences, and used the literature to test three hypotheses, namely, that the behavioural changes were a simple social facilitation effect, that they were the consequence of the audiences being stressful to the animals, and that they were the consequence of the audiences being enriching for the animals. The evidence mostly supported the stressful hypothesis, with some support for the hypothesis that audiences could under some circumstances be enriching, and with no support for the facilitation hypothesis. However, inconsistencies were noted in the behavioural responses recorded in different studies, and it was suggested that these might be the result of differences between species, between housing conditions, and in the way different audiences were perceived. It is also worth pointing out that many of the published studies show an association between the behaviour of the animals and the presence of visitors, but do not necessarily indicate unequivocally the direction of causality. Thus, it is also possible to argue that the animals show elevated activity and agonism for some other reason, and that this greater activity in the cage attracts the audience (Mitchell et al., 1992c). This, for example, was considered by Margulis et al. (2003) to be the best explanation of associations they saw between felid behaviour and visitor presence.

The studies reviewed by Hosey (2000) were overwhelmingly primate studies; while this is still the case with the literature, there are now many more studies available, and they show that the situation is even more complex when non-primate studies are available. The available studies are briefly reviewed here by taxonomic group in order to detect whether any trends or differences are apparent between different kinds of animal.

4.3. Primates

Studies which have involved primates are shown in Table 1 (lemurs and monkeys) and 2 (apes). Looking at the lemurs and monkeys first, there appears to be a reasonable consistency in what the different studies show. In most cases the animals show an increase in locomotion or activity (one redfronted lemur shows a decrease), an increase in agonistic behaviour (but not in the black lion tamarin or the green monkey) and a decrease in grooming and/or affiliative behaviours (but not in the mangabey). This is the suite of behavioural changes that was first suggested by Chamove et al. (1988) to indicate stressful excitement in the animals, and many subsequent studies have followed this interpretation. What about the exceptional cases?

The black lion tamarin *Leontopithecus chrysopygus*, shows no increase in agonistic behaviour, unlike most of the other species. The authors of that report attributed this to a species characteristic, that these were a much ‘‘more relaxed’’ species when visitors were present (Wormell et al., 1996). In Fa’s (1989) study of green monkeys *Cercopithecus aethiops sabaeus* at Mexico Zoo no increases in agonistic behaviour were seen, but these animals were being fed by the public, so zoo visitors may not have been seen as stressful by the animals. Indeed, visitor-directed behaviours in this group were related to obtaining food. In most of the other studies visitor-directed behaviours have not been scored; the mangabeys *Cercocebus galeritus chrysogaster* showed elevated intra-group agonistic behaviour and also directed threats at the visitors (Mitchell et al., 1991a, 1992a), whereas the mandrills *Mandrillus leucophaeus* increased their rates of glancing at the visitors as visitor numbers increased, which again was interpreted as a stressful effect of people on the animals (Chamove et al., 1988).

Studies on the behaviour of apes when human visitors are present are summarised in Table 2. This is the biggest collection of studies for any taxonomic group, but it does include some laboratory animals (Lambeth et al., 1997; Rumbaugh, 1988; Maki et al., 1987) as well as those in zoos. This raises the possibility of examining intra-species as well as inter-species variability in behavioural responses to humans. Visitor-directed behaviour has been a behavioural measure in most of these studies, and only one (Mather, 1999) looked for visitor-directed behaviours and found none. For the rest, the visitor-directed behaviours include those which may indicate that visitors were a source of stress (looking at visitors, turning their backs on them, or aggressively threatening them), but there are also two studies here which suggest that the animals were not stressed by people. In one of these a gorilla at Antwerp Zoo (but not the other four animals in the cage) spent a great deal of time at the glass viewing window when audiences were present, and appeared to seek interaction with them (Vrancken et al., 1990). In the other, chimpanzees at Chester Zoo appeared to be willing to engage in sequences of non-aggressive interactions with members of the public (Cook and Hosey, 1995). Thus, we see intra-specific variation in visitor-directed behaviours in both gorillas (even within the same group in this case) and chimpanzees.

Table 1
Behavioural changes associated with the presence of zoo visitors in various primate species (excluding apes)

	Visitor-directed behaviour	Locomotion/ activity	Agonistic behaviour	Grooming	Affiliative/ friendly	Other
Lemur catta[a]		Increase	Increase	Decrease		
Eulemur fulvus mayottensis[b]	Yes, but not described	Increase				
Eulemur fulvus rufus[c]	One animal grabbed at a plant pushed through the wire	Decrease				
Varecia variegata[d]		Increase				
Saguinus oedipus[e]			Increase		Decrease	
Saguinus oedipus[a]		Increase	Increase	Decrease	Decrease	
Saguinus bicolor[f]			Increase			
Leontopithecus chrysopygus[f]			No effect			
Cebus xanthosternos[g]		Increase			Decrease	
Cercopithecus diana[a]		Increase	Increase	Decrease	Decrease	
Cercopithecus diana[h]				Decrease		Increase in feeding and playing, decrease in resting
Cercopithecus aethiops[i]	Increase in feeding-related behaviour	Increase	No effect	Decrease		
Cercocebus galeritus[j]	Increase in threats		Increase	No effect	No effect	
Mandrillus leucophaeus[a]	Increase in glancing at visitors	Increase				Increase in abnormal
Macaca silenus[k]			Increase		Decrease	Increase in abnormal

Sources are:
[a] Chamove et al. (1988).
[b] Hosey (1989).
[c] Jeffery and Price (2004).
[d] Hutchings and Mitchell (2003).
[e] Glatston et al. (1984).
[f] Wormell et al. (1996).
[g] Hague (2005).
[h] Todd et al. (2007).
[i] Fa (1989).
[j] Mitchell et al. (1992a,b,c).
[k] Mallapur et al. (2005).

Table 2
Behavioural changes in apes associated with the presence of zoo visitors

	Visitor-directed behaviour	Locomotion/activity	Agonistic behaviour	Grooming	Other
Hylobates leucogenys[a]	Aggressive behaviour			♀ less ♂ no effect	
Hylobates syndactylus[b]	Hostile behaviour	Decrease			
Hylobates pileatus[c]					Increase in stereotypy
Pongo pygmaeus[d]	No	Increase		No effect	
Pongo pygmaeus[e]	Increase in looking at visitors	Decrease			Decrease in feeding/foraging
Pongo pygmaeus[f]	Increase in looking at visitors				Hide, avoid
Gorilla gorilla[g,h]		Increase	Increase		Increase in stereotypy; hide and avoid
Gorilla gorilla[i]	Aggression and turning back to glass	Decrease			Hide and avoid; decrease in feeding/foraging
Gorilla gorilla[j]	1 animal increased eye contact and mouth movements				No hide and avoid
Pan troglodytes[k] *(lab)*			Increase		
Pan troglodytes[l]		No effect		Decrease	No effect on stereotypy; decrease in feeding/foraging
Pan troglodytes[m] *(lab)*	Aggression				
Pan troglodytes[n]	Aggression	Increase	Increase	Increase	
Pan troglodytes[o] *(lab)*	Yes		Increase		
Pan troglodytes[p]	Begging, eye contact, vocalisation				

Sources are:
[a] Lukas et al. (2002).
[b] Nimon and Dalziel (1992).
[c] Skyner et al. (2004).
[d] Mather (1999).
[e] Jones and Wehnelt (2003).
[f] Birke (2002).
[g] Wells (2005).
[h] Blaney and Wells (2004).
[i] Keane (2005).
[j] Vrancken et al. (1990).
[k] Lambeth et al. (1997).
[l] Wood (1998).
[m] Rumbaugh (1988).
[n] Perret et al. (1995).
[o] Maki et al. (1987).
[p] Cook and Hosey (1995).

Similar intra-specific variation is seen for some of the other behavioural measures used in these studies, and notably for activity and grooming.

4.4. Felids

Studies on the behavioural changes of felids associated with the presence of zoo visitors are summarised in Table 3. There is consistency in the cats' lack of change in activity levels, with one study showing a decrease (Mallapur and Chelan, 2002) and none showing an increase. If activity is taken to be a suitable measure, then this would seem to imply either that cats are not greatly disturbed by the presence of people, or that if they are they do not manifest it in changes in their activity. Again, stereotypy or pacing does not seem to be much affected by the presence of visitors, with the exception of the jaguar in the study by Sellinger and Ha (2005), which showed an increase in pacing as visitor numbers increased, followed by a decrease in pacing as numbers got higher. In the study by Mallapur and Chelan (2002), the leopards showed less stereotypy when on-exhibit, which the authors attribute to enclosure characteristics rather than visitor presence. In general felids appear to show much less behavioural change when confronted with unfamiliar people than is the case with primates.

4.5. Spheniscids

Several studies have looked at audience effects in penguins (Table 4); the measures are somewhat different here, reflecting different research aims in these studies. One study (Warren et al., 2002) found a visitor-related increase in activity in both the gentoo *Pygoscelis papua* and black-footed penguin *Spheniscus demersus*, but a different study (Brooking and Price, 2004) looking at the same two species only found a decrease in resting (almost the converse of activity) in one of them, the black-footed penguin. The data are rather sparse, and there are no real trends discernable.

Table 3
Behavioural changes in felids associated with the presence of zoo visitors

	Activity	Stereotypy/pacing	Visible	Rest	Alert
Felis viverrinus[a]	No effect				
Neofelis nebulosa[a]	No effect				
Acinonyx jubatus[b]	No effect				
Panthera uncia[a]	No effect				
Panthera uncia[c]		No effect		Increase	Increase
Panthera pardus[c]		No effect			
Panthera pardus[a]	No effect				
Panthera pardus[d]	Decrease	No effect, but less on-exhibit		Increase	
Panthera onca[c]		No effect			
Panthera onca[e]		Decrease	Decrease		
Panthera leo[a]	No effect				
Panthera tigris[a]	No effect				

Sources are:
[a] Margulis et al. (2003).
[b] O'Donovan et al. (1993).
[c] Cunningham (2005).
[d] Mallapur and Chelan (2002).
[e] Sellinger and Ha (2005).

Table 4
Behavioural changes in penguins associated with the presence of zoo visitors

	Activity	Use of pool	Resting alert	Resting non-alert
Pygoscelis papua[a]	Increase			
Pygoscelis papua[b]			Increase	Increase
Spheniscus demersus[b]			Decrease	Decrease
Spheniscus demersus[a]	Increase			
Spheniscus humboldti[c]		No effect		

Sources are:
[a] Warren et al. (2002).
[b] Brooking and Price (2004).
[c] Clarke (2003).

4.6. Other taxa

Several other studies covering a miscellaneous array of species have been published and are summarised in Table 5. The first two studies look at visitor-related behavioural change in three species of parrot. We might expect parrots to be similar to primates in their responses to unfamiliar humans, but there are few data available in the literature to discern any real trends. The authors of both of the studies listed here considered that human audiences have an enriching effect for at least some of the birds. One of the studies (Nimon and Dalziel, 1992) observed a single long-billed corella *Cacatua tenuirostris*, who appeared to seek out opportunities to interact with human visitors, putting particular effort into interactions on quiet days when fewer people

Table 5
Behavioural changes in various species associated with the presence of zoo visitors

	Visitor-directed behaviour	Locomotion/ activity	Agonistic behaviour	Play	Forage/ feed	Position in cage
Cacatua sulphurea[a]		Increase				Front
Cacatua moluccensis[a]						Back
Cacatua tenuirostris[b]	Face-to-beak contact/vocalisation					
Macropus rufogriseus[c]		Decrease			Increase	
Aonyx cinerea[d]	Begging/vocalisation			Increase	Increase	
Diceros bicornis[e]		Increase in pacing				
Sus scrofa[f]	None					
Capra hircus[f]	Aggression/avoidance					
Capra hircus[g]	Aggression/avoidance					
Ovis aries[f]	Aggression/avoidance					
Ovis aries[g]	Aggression/avoidance					
Gazella soemmeringii[h]			Increase			

Sources are.
[a] Keane (2005).
[b] Nimon and Dalziel (1992).
[c] Lockley and Leadbeatter (2005).
[d] Owen (2004).
[e] Burrell et al. (2004).
[f] Lacey and Pankhurst (2001).
[g] Anderson et al. (2002).
[h] Mansour et al. (2000).

were present in the zoo. In the other study (Keane, 2005), two citron-crested cockatoos *Cacatua sulphurea citrinocristata* housed close to a children's play area increased their activity but also the number of positive social behaviours they showed to each other when the playground was busy, whereas two Moluccan cockatoos *Cacatua moluccensis* increased their vocalisations. The citron-crested cockatoos spent more time at the front of the cage when the children were present, and the author considered that proximity to the playground was enriching for them, but not for the Moluccan cockatoos, who spent more time at the back of the cage.

The two *Capra*/*Ovis* studies report very similar results to each other, showing good consistency. In both the sheep and the goats were in petting areas, and both showed an increase in aggression towards and avoidance of visitors as visitor numbers increased. The study of three short-clawed otters *Aonyx cinerea* shows an increase in play and feeding/foraging, as well as behaviours such as begging directed at zoo visitors. The author of this study (Owen, 2004) considered that the audience had a positive effect on the otters.

4.7. A model

There are now sufficient studies across a range of taxa to show that the responses zoo animals show to unfamiliar humans (i.e. zoo visitors) are not particularly consistent between, and sometimes within, taxa. Many studies, for example, appear to show that zoo visitors may be stressful to primates, in as much as their presence is associated with increases in the animals' activity and within-group agonistic behaviour, and decreases in more affiliative behaviours such as grooming. But different studies for the same species in different zoos (such as gorillas and chimpanzees) show some variability, with not all individuals showing the same behavioural change. Similarly, the behaviours directed at visitors sometimes indicate stress, but in some cases imply that the animals are not stressed and may even be enriched. Moreover, if our earliest studies had been on felids rather than primates we may well have concluded that zoo animals were not affected by visitors at all. Understanding why these animals show the responses they do is of some importance to us, as they potentially impact on the animals' welfare and conservation (Ross et al., 2007), but also might contaminate other research results based on the behaviour of zoo animals (Hosey, 2000). Furthermore, it would be beneficial if zoos could provide visitors with an experience of animals which enhanced their visit, including possible scope for interaction with the animals, and this again would need to be concordant with the welfare of the animals and hence take account of what the interactions mean to the animals. Thus, we need to develop a framework or model to help us interpret these responses, and the rest of this paper is devoted to a preliminary attempt to outline such a model. It is preliminary in the sense that it is untested and, in the absence of relevant research data, probably does not contain all of the variables which will turn out to be important. It is presented here as a possible way forward in gaining appropriate empirical data, in the hope that it will be refined as human–animal relationships are explored more thoroughly in zoo settings. The model incorporates features of the HAR concept as developed for farmed animals, and includes zoo visitors as an additional variable. It is based on the assumption that zoo animals develop HARs with both familiar and unfamiliar people, and the hypothesised effects of these on the animals are shown in Table 6. The model based on these is shown in Fig. 1.

4.8. Animals' species-specific fear of humans

The starting point, as with Hemsworth (2003) model for farmed animals, is with the animals' fear of humans. If we can conceive of this as a basic motivation in farmed animals, even after a

Table 6
Matrix summarising the possible pairs of HARs which zoo animals may develop with familiar and unfamiliar people

Familiar humans	Unfamiliar humans		
	Positive HAR	Neutral HAR	Negative HAR
Positive HAR	Low fear, confident with/enriched by people	Low fear, indifferent to people	Low fear with keepers; high fear with unfamiliar people
Neutral HAR	Low fear, avoid contact	Low fear, avoid contact	High fear, avoid contact
Negative HAR	High fear, avoid contact	High fear, avoid contact	High fear, stress

The cells describe the hypothesised characteristics of the animals with respect to their interactions with humans that result from these HARs.

long process of domestication, then it must certainly be a significant influence on the responses of zoo animals to humans. The intensity of this motivation is presumably much more variable for zoo animals simply because of the greater range of kinds of species compared with the farm. Thus, not all species will start to interact with people in the zoo from the same starting point.

How species differences affect fear of humans is not clear. Although much research has been undertaken on fear in animals (Boissy, 1995), much of it is concerned with intra-specific rather than inter-specific variability. Hediger (1965, 1970) referred to the fear of humans in terms of the animal seeing the human as ‘‘an enemy’’, and considered that they would then flee if people came within their ‘‘flight distance’’. To try to apply this across broad taxonomic categories (e.g. ungulates should show more fear because they are prey species) is almost certainly simplistic, as the limited evidence shows that taxon differences are likely even in closely related species. For example, young baboons are less fearful of humans than young rhesus monkeys of the same age (Maple, 1974). In a study of petting zoo animals (Anderson et al., 2002) the authors deliberately selected for observation pigmy goats and Romanov sheep because these were characterised in the literature as amiable (the goats) and fearful of humans (the sheep), respectively. Because of this the authors expected, and found, a higher rate of undesirable behaviours (aggression, avoidance) in the sheep than in the goats when zoo visitors were present. So the small amount of evidence that is available suggests that different species of animals in zoos are likely to differ in their fear of humans, but this is an area where further research is clearly needed.

4.9. Interactions with familiar and unfamiliar humans

The interactions that zoo animals have with familiar people (usually keepers) are probably both qualitatively and quantitatively different from those they have with unfamiliar people. Keepers are individually familiar because they daily spend a lot of time with the animals, and within this context a lot of interactions are possible. These may, of course, include both positive (e.g. feeding) and negative (e.g. catching for veterinary inspection) interactions. Zoo visitors, on the other hand, are individually unfamiliar because each is present for a very short period; however, it is possible that animals generalise experiences with individual visitors (and perhaps also interactions with keepers) to visitors as a whole, so that the total number of interactions with zoo visitors may be quite high. Such generalisation might be related, amongst other things, to the ease with which the animals can discriminate between different categories of people. So, to what extent are animals able to discriminate between different kinds of people, or even individual people?

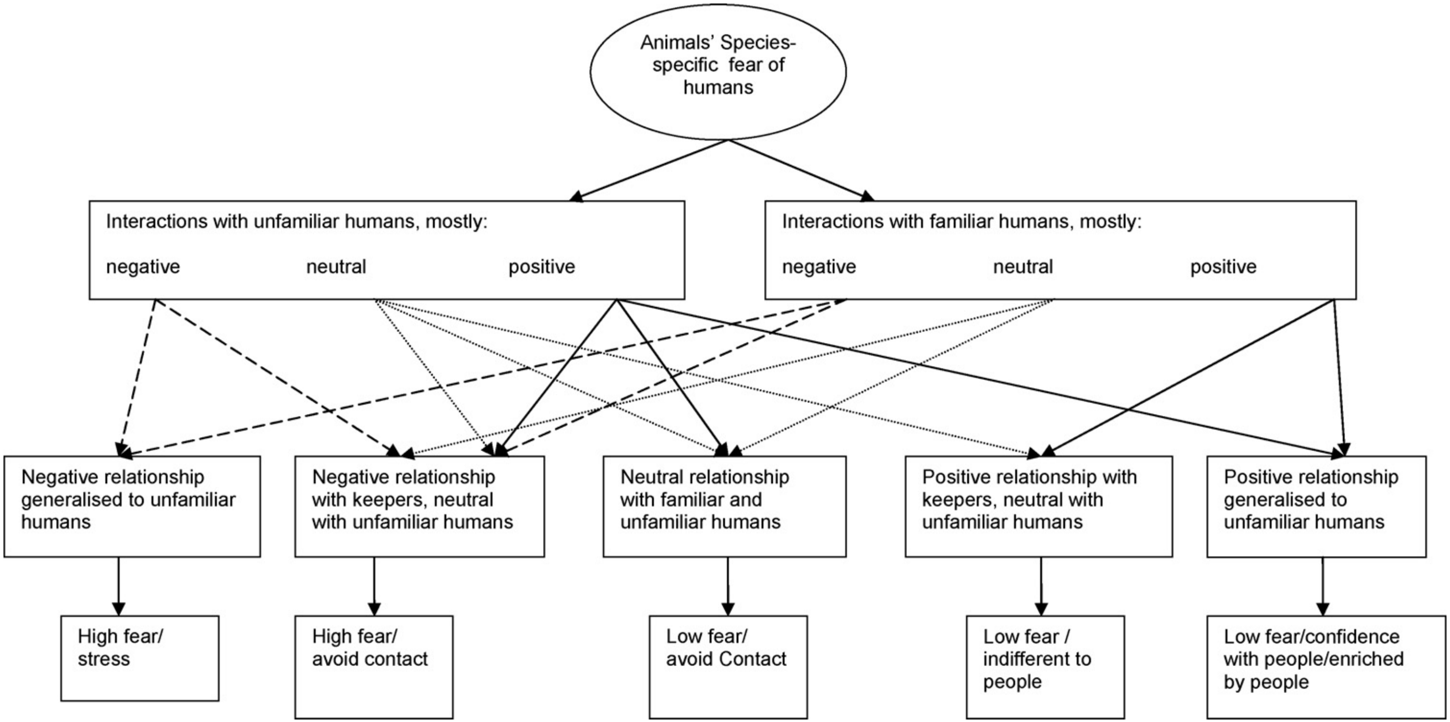

Fig. 1. A model of human–animal interactions and their consequences for human–animal relationships (HARs) in zoo animals. The starting point is the animal's fear of humans, the extent of which is dependent upon the animal's species. A history of mostly positive or negative interactions with people serves to decrease or increase that fear, and leads to the establishment of relationships which reflect the animal's perceptions of humans. Arrows are drawn differently simply as an aid to visual clarity. The relationships shown range from most negative on the left to most positive on the right. See text and Table 6 for further details.

There is evidence from both the agricultural and the laboratory literature that animals can distinguish familiar and unfamiliar handlers. Calves, for example, behave differently towards familiar and unfamiliar handlers (Rousing et al., 2005) and towards different handlers dependent upon their previous interactions with them (De Pasillé et al., 1996) and with their usual caretaker (Boivin et al., 1998). They can, furthermore, develop a general fear of people if subjected to rough handling, although positive handling can overcome this (De Pasillé et al., 1996). A number of cues including clothing (Rybarczyk et al., 2003; Munksgaard et al., 1999) and facial features (Rybarczyk et al., 2001) allow them to make these discriminations. Rabbit pups also appear to be able to distinguish between people according to how much they are handled (Csatádi et al., 2007). According to Davis (2002) the ability to discriminate between humans has been shown in rats, chickens, llamas, rabbits, sheep, cows, seals, emu, rhea, penguins and honeybees. There is even anecdotal evidence that reptiles (Bowers and Burghardt, 1992) and octopus (Mather, 1992) can show discrimination between categories of people.

What about animals in zoos? Hediger (1970) gives anecdotal examples of zoo animals such as tigers and shoebills *Balaeniceps rex* recognising and greeting their keepers, but few quantitative studies have been undertaken. Mitchell et al.'s investigations of mangabey–human interactions at Sacramento Zoo show that the animals behave differently towards keepers, observers and the public (Mitchell et al., 1991a), and also to different age/sex categories of zoo visitors (Mitchell et al., 1992b). Similarly colobus monkeys show different frequencies of human-directed behaviours towards keepers, other zoo workers and the public (Melfi and Thomas, 2005). Again, there is a need here for more research on the extent to which animals in zoos distinguish different categories of people, and how much they generalise their interactions across these categories.

4.10. Negative, positive and neutral interactions

There is a general consensus in the farm animal literature about what constitutes different qualities of interaction (Waiblinger et al., 2006; Hemsworth, 2003; Boivin et al., 2003; Rushen et al., 1999). Negative interactions can include hits, slaps, shouting and fast speed of movement (Hemsworth, 2003), and generally rough, aversive and/or unpredictable handling (Waiblinger et al., 2006). Positive interactions include feeding and petting (Boivin et al., 2003), and positive use of verbal and physical effort (Hemsworth, 2003). These are all part of the day-to-day interactions with the stockperson, and stockpeople show differences, which are related to their attitudes and personality, in whether their interactions are predominantly positive or negative (Waiblinger et al., 2002). Of course, there are other interactions which can also be aversive, for example restraint and veterinary treatment (Waiblinger et al., 2006), and which may not occur on a day-to-day basis.

We know virtually nothing of how this applies in the zoo setting. One of the few empirical investigations of differences in stockperson (keepering) styles involved a comparison of three different rhinoceros keepers at Paignton Zoo (Ward and Melfi, 2004). All three keepers showed primarily positive interactions, but differed in the number of negative interactions they initiated. This was reflected in different latencies showed by the animals when required to move by the different keepers. Keeper interactions with tigers in an interactive zoo exhibit also differed between keepers and involved both positive (playing, patting) and less positive (hitting) interactions; these were related more to keeper than tiger personalities (Phillips and Peck, 2006). In the few other studies where keeper–animal interactions have been considered, negative and positive interactions have generally not been documented, but general-purpose categories of positive style have been erected, based on time spent with the animal, and/or talking to the animal (Mellen, 1991; Baker, 2004).

Here, again, there is a clear need for empirical research, to establish what differences there are in keepering styles, how these relate to keeper characteristics, and what effects they have upon the behaviour (and indeed other life history characteristics: see Mellen, 1991) of the animals. We must recognise, however, that human–animal interactions in zoos are not restricted to those they have with their keepers; they are also likely to interact with other zoo personnel, contractors brought in for routine maintenance and building work, and the visiting public. There appear to be no empirical studies of human–animal interactions involving the first two categories, and very few involving the third.

Mitchell et al. (1992c) investigated threats shown by mangabeys and human visitors to each other at Sacramento Zoo. Infants of both human and mangabey were rarely involved in harassment. Men and boys, however, threatened the male mangabeys significantly more than they threatened the females, and significantly more than women and girls did. This may reflect something like Hediger's category ''animals viewing humans as a conspecific'' acting for humans as well, or it may represent something more general about human gender differences in attitudes and behaviour to zoo animals. We do not know. Not all visitor–animal interactions are so negative. Cook and Hosey (1995) showed that chimpanzees and human visitors at Chester Zoo were willing to engage in relatively long sequences of interactions which were characterised by fairly neutral behaviours such as eye contact, making noises and gestures, and begging for/offering food. Similarly a long-billed corella (*Cacatua tenuirostris*) at Adelaide Zoo made great efforts to interact with humans, although unfortunately the behaviour of the humans was not recorded (Nimon and Dalziel, 1992). Thus, animals in zoos build up a history of interactions with a mixture of familiar and unfamiliar people. What sorts of relationships are set up as a result?

4.11. Relationships

In the agricultural literature, the relationships that are set up as a result of interactions between animals and stockpersons may be positive, neutral or negative. These have been characterised (Waiblinger et al., 2006) as low fear of humans or high levels of confidence in people (positive HAR); low fear of humans but animals avoid contact (neutral HAR); and high fear of humans where animals avoid contact and may show stress (negative HAR). It is not only the quality of interactions, but also the quantity of each kind of interaction which results in one of these HARs. The neutral HAR, for example, can develop not just from a history of neutral interactions, but also from mildly positive contact, a lack of negative contact, and few (or none) intensely positive contacts (Waiblinger et al., 2006). Similarly, presence of a familiar person with whom the animal has a positive HAR can be calming for the animal when exposed to negative events (Waiblinger et al., 2006). In Fig. 1 this complex relationship between quality and quantity of interactions is shown simply as ''mostly'' positive, neutral or negative, without any implication that it really is that simple.

In the zoo setting this picture is complicated by the fact that the history of interactions an animal has with familiar people (notably keepers) may be similar to or different from the history of interactions it has with the public. In the simplest case we can imagine that the animal generalises all of these interactions to achieve one general-purpose HAR with people. The most complex case would be where the animal discriminates between all individual people, though it is difficult to see a HAR developing with members of the public who are present for just minutes. Within the model outlined here it is assumed, on the basis of evidence described above, that the animal can discriminate between familiar (keepers) and unfamiliar (visitors) humans, and forms a generalised HAR at least with the latter. In this case, the animal is likely to have HARs with familiar and (generalised) unfamiliar humans. The possible combinations of these are shown in Table 6.

The characteristics of the animals in each of these HAR combinations are not known. The combinations positive–positive, neutral–neutral and negative–negative are based on the characteristics of farmed animals in positive, neutral and negative relationships described by Waiblinger et al. (2006). The other cells are more speculative, and are based on an assumption that the interactions with familiar humans will be more powerful determinants of the animal's HARs than those with unfamiliar people. If this is the case, then a negative HAR with keepers can be hypothesised to result in animals with high fear of humans regardless of their past interactions with the public, whereas a positive HAR with keepers may lead to low fear with people, unless the HAR with unfamiliar people is negative, in which case we can suggest that the animal may discriminate between these two categories of people (if it is able to) and show low fear with familiar, but high fear with unfamiliar people. In any case, the worst situation for the animal is likely to be when it has negative HARs with both familiar and unfamiliar people. Similarly, the best situation is where the animal has a positive HAR with both familiar and unfamiliar people, which may result in the animal being confident with, and possibly enriched by, human presence.

4.12. *Other factors*

Species differences have already been mentioned as a variable that will affect the initial fear of the animal towards humans, and we can add that they may also affect the degree to which negative or positive interactions are actually perceived by the animal as negative or positive, and hence lead to between-species variability in the way these interactions influence behaviour. Other variables are also likely to moderate the basic development of HARs in zoo animals, but are not incorporated into the model shown in Fig. 1. Enclosure design is probably important because it can influence the behaviour of the animals in so many ways. Cotton-topped tamarins, for example, show less within-group amicable behaviours when housed in small, glass-fronted cages than when in larger, wire mesh-fronted cages (Glatston et al., 1984). Similarly, activity is increased in great apes when enclosure complexity is increased (Wilson, 1982; Perkins, 1992). An important feature of enclosure design is the amount of control it gives the animal over the extent to which it is exposed to humans. Where opportunities are available for animals to retreat from the public they do make use of them (Mallapur et al., 2005; Anderson et al., 2002) and provision of hiding places to leopard cats leads to a decline in their urinary cortisol, indicating the cats are less stressed (Carlstead et al., 1993). Thus, enclosure design probably influences, not the fear of the animal, but the extent to which interactions are perceived as positive or negative.

A further variable which is likely to influence the establishment of the HAR in zoo animals is the extent of handling it experiences during its early life. In agricultural animals there is some evidence for a sensitive period soon after birth in which social attachments are made, usually to the mother, but sometimes to the stockperson. Thus, early handling can reduce the animal's fear of humans in calves (Krohn et al., 2001, 2003), lambs (Boivin et al., 2000; Tallet et al., 2005), pigs (Hemsworth and Barnett, 1992) and rabbits (Csatádi et al., 2005). How this affects zoo animals is not known, though warnings have been raised about the adverse effects on reproduction of raising small felids with only human contact (Mellen, 1992). In any case, handling, provision of food, and probably many other kinds of interaction will characterise the development of the zoo animal's relationship with its keepers, but not with unfamiliar members of the public.

Other variables affecting HAR development, which again are not incorporated into Fig. 1, include individual differences in the temperament and personality of the animal. For example, Phillips and Peck (2006) found that the personalities of tigers influenced the ways they interacted with keepers, and friendliness to keepers has been identified as a component of black rhinoceros individual differences (Carlstead et al., 1999).

5. Testing the model

There are no data available at present to test the model, but the model can make various predictions which are amenable to testing by future researchers. Among the predictions of the model are the following:

(i) there will be species differences in the fear responses zoo animals show to humans. Although the studies summarised in Tables 1–5 show apparent differences between species, it is not clear how these should be interpreted because they generally involve a small number of individuals, they cover a range of housing conditions, and they are primarily responses to interactions generated by unfamiliar people. Again, researchers on farmed animals have developed a number of methods for detecting fear responses (see, for example Waiblinger et al., 2006), and many of these could be applied in the zoo setting. They include measuring animals' reactions to stationary humans, moving humans and actual handling, including routine handling; measures include avoidance and ease of handling. Such tests should be interpreted with due attention to the likelihood of individual differences within each species.

(ii) there will be differences between keepers in the relative frequencies of positive and negative interactions directed towards the animals. Data to test this can be gained from observational studies of keepers during routine day-to-day interactions, such as moving and feeding animals.

(iii) there will be relationships (HARs) of different quality between individual animals and different keepers; these should correlate with different keepering styles as measured in (ii) above. The farm animal literature contains a great deal of information on methods of assessing the HAR, and much of this is reviewed by Waiblinger et al. (2006).

(iv) animals are more likely to show low fear of humans if they are maintained in enclosures which give them at least some control over whether or not they interact with unfamiliar humans. This is because allowing them choice can reduce the frequency of negative interactions they are subjected to, and may also change their perceptions of how negative an interaction is. Single-species comparisons across a variety of enclosure types are needed for this.

(v) animals which have a history of mostly negative interactions will show higher fear of humans, particularly unfamiliar humans. This prediction, which would perhaps be the most powerful test of the model, can, of course, also be reformulated in terms of the other possible histories of interaction. Obtaining measures of the animals' past history of interactions is difficult: possible measures, albeit indirect, might include the number of veterinary treatments the animal has had, the number of past transfers between enclosures or between zoos, the number of different keepers with which it has had regular interaction, their methods of handling, moving or catching animals, and whether training has been used (and if so, whether with positive or negative reinforcement).

(vi) an increase in the number of positive interactions for an individual animal should increase the positivity of its HARs, and thus reduce the aversive effect of unfamiliar people on the animal's behaviour. The study by Melfi and Thomas (2005), discussed above, supports this prediction, as one of the effects of positive reinforcement training on the colobus monkeys was a decrease in their responsiveness to humans.

6. Usefulness of the model

This model is offered here as a possible way forward in understanding and interpreting human–animal interactions in the zoo, and in the hope that it will stimulate new research to enhance our management of zoo animals. If the general validity of the model is supported by future research, then perhaps we can again follow the lead given by the agricultural researchers in applying this knowledge to enhance animal welfare in the zoo. The way to do this is to attempt to increase the net-positive quality of human–animal interactions in the hope that positive, or at least neutral, HARs are set up between animal and keeper, and maybe even animal and zoo visitor. It is probably the case that zoos will have limited scope to influence the quality of visitor-initiated interactions, although educational experiences such as keeper talks and animal shows may play a role here (e.g. Anderson et al., 2003), and simple manipulations such as the use of camouflage netting can have beneficial effects on animal behaviour and on visitor perceptions (Blaney and Wells, 2004). Zoos do, however, have some influence on keeper skills and behaviour, an area which has been prominent in the agricultural research (Hemsworth, 2003; Boivin et al., 2003). Techniques such as positive reinforcement training also offer much potential for increasing the positivity of human contact for captive animals (Savastano et al., 2003; McKinley et al., 2003). Ultimately we may know enough about the dynamics of human–animal interactions in the zoo context to be able to ensure the best welfare of the animals while still providing a positive and rewarding experience both for the people who work with those animals and the zoo-visiting public on whom most zoos depend.

Acknowledgments

The ideas expressed here were developed for a talk at the Zoo Animal Learning and Management Workshop at Paignton Zoo, and I thank Vicky Melfi for inviting me to do the talk and providing comments on a draft of the manuscript. I am grateful to Jon Amory for his comments on the manuscript, and for helping me to avoid saying anything silly about agricultural animals. I thank the anonymous reviewer, whose detailed comments helped to greatly improve the model and the paper.

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