Hediger Revisited: How Do Zoo Animals See Us?

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Contact with people, both familiar (e.g., caretakers) and unfamiliar (e.g., members of the public), is a significant part of the lives of nonhuman animals in zoos. The available empirical evidence shows that in many cases this contact represents a source of stress to the animals, although there is sufficient overall ambiguity in these studies to suggest that the effect of people on the animals is much more complex than this. A possible way to try to understand human-animal relationships in the zoo is to ask how the animals might perceive the humans with whom they have contact, and here this question is explored further, using a framework first published by Hediger as a starting point. Hediger suggested that zoo animals might perceive people as an enemy, as part of the inanimate environment, or as a member of the same species. He supported these categories with anecdotal evidence, which was all that was available at the time, but more empirical evidence is available now, so it is appropriate to revisit these categories. The evidence suggests that animals discriminate both conspecific and heterospecific others, rather than just viewing familiar people as members of their own species, and that additional categories (stimulating part of the environment and friendship) may be warranted. These categories are then placed in a general model that suggests how relationships of different qualities, and hence different perceptions of each other, might develop between animals and the people they are in contact with in zoos.

Keywords: human-animal interaction, human-animal bond, visitor effect

How do nonhuman animals in the zoo see us? This was asked more than 40 years ago by Hediger (1965, 1970), one of the founders of modern zoo biology, using anecdotal evidence from his many years as Director of Zurich Zoo. He identified five ways in which humans could have significance to animals. We now have more extensive empirical evidence of the sorts of interactions zoo animals have
with people, so it is feasible to approach the question in a more systematic way, and here I attempt to do that by revisiting Hediger’s categories.

**DEFINITIONS**

First, some definitions. When I refer to zoo animals here, I am really talking about nonhuman mammals. Trying to understand how other mammals perceive us is difficult enough, but it is likely to be even more difficult with the other vertebrates, and it is hard to know even where to start with invertebrates. In any case, nearly all the evidence we have comes from mammals and indeed mostly from primates. The term *interaction* is used here in the way defined by Hinde (1976), as “a sequence in which individual A shows behavior X to individual B, or A shows X to B and B responds with Y” (p. 3). This definition allows us to determine that an interaction has taken place by observing the behavior of the actor or the recipient and thus allows us to ignore unknowables such as intention or motivation. A “relationship” is then the result of a series of interactions in time between two individuals known to each other, with the assumption that each interaction affects the future course of the relationship (Hinde, 1976).

So, when particular animals and people have a history of interactions such that they can to some extent anticipate how the other is going to behave, we can assume that a human-animal relationship (HAR) has been established. To an observer, the presence of HARs manifests itself as predictability in the interactions shown within a dyad and differences shown with other dyads that involve one of the same interactants. From the starting point of Hinde’s (1976) definition of interactions, we would expect HARs to be established between individual animals and individual people, but it is also possible to conceive of a generalized HAR between one person and a group of animals, or one animal and a group of people, if the experience of one human is generalized to other humans or one animal to other animals.

This concept of a generalized HAR is commonly used in the literature on agricultural animals (Hemsworth & Coleman, 1998; Jones, 1994; Waiblinger et al., 2006) and can be applied in the zoo setting as well. Thus, we might expect that zoo animals are more likely to have generalized HARs with unfamiliar people such as zoo visitors and individual HARs with familiar people such as caretakers.

**HEDIGER: “WHAT DOES MAN MEAN TO THE ANIMAL?”**

Hediger (1965, 1970) identified five ways in which humans could have significance for animals: as an enemy, a prey, a symbiont, a part of the inanimate
environment, and as a member of the same species. Fortunately (for us) cases of animals perceiving humans as prey appear to be rare, although they do occur, both in the wild and in captivity (Grice, 2010). Hediger did not offer any examples within the zoo context, and this category is not considered any further here. Similarly, symbiotic relationships (in the sense of partnerships between humans and animals) are also rare, and again Hediger did not give any zoo-based examples, so this category is also not considered here. This leaves us with three ways in which zoo animals might perceive humans.

Humans as an Enemy

Hediger (1970) considered humans being the enemy the most common category, and he viewed humans as a sort of universal enemy from which animals would escape if a person came within the animal’s flight distance. It is not clear why this is the case, but the implication is that humans are viewed as predators. Certainly, a large amount of literature on HARs in agricultural animals takes the animals’ fear of humans as its starting point, and models of how HARs develop in agricultural animals incorporate the idea that a history of human-animal interactions can either increase or decrease that fear, depending on the quality of the interactions (Hemsworth, 2003; Waiblinger et al., 2006). But the fear of humans is assumed for other predators as well, such as bears, wolves, and foxes (McCullough, 1982; Rekilä, Harri, & Ahola, 1997; Woolpy & Ginsburg, 1967). Because of this belief in the universality of animals’ fear of humans, models of how zoo animals respond to people also use this as their starting point (Hosey, 2008).

The model proposed by Hosey (2008) predicts that different species will have different levels of fear of humans and will therefore exhibit differences in their responses to humans. There is some evidence for this. Young baboons were less fearful of humans than young rhesus monkeys of the same age (Maple, 1974), and gibbons showed no fear of humans at all (Bernstein, Schusterman, & Sharpe, 1963). More recently, Carlstead (2009) demonstrated species differences in fear of humans in several species of zoo animal, with maned wolves and black rhino being most fearful, the great hornbill being the least fearful, and the cheetah in between.

Free-ranging animals’ responses to humans’ approach may manifest in their alert distance (the distance between an animal and an approaching human at which point the animal begins to exhibit alert behaviors to the human) or their flight-initiation distance (the point at which they attempt to escape; Fernández-Juricic, Jimenez, & Lucas, 2001), which appears to be a species-specific trait (Blumstein, Anthony, Harcourt, & Ross, 2003). Free-ranging animals respond to their predators this way, with alertness and flight, as well as to approaching humans. The reduced ability of captive animals to escape from the proximity of
humans (and perhaps of other animals as well) can be a significant source of stress for them (Morgan & Tromborg, 2007).

Humans as a Part of the Inanimate Environment

The examples given by Hediger show that what he meant was that animals might sometimes use people as substrates on which to settle, run, or climb. Hediger (1970) gave descriptions of birds using keepers’ heads and outstretched arms as perches and of a koala climbing up a person’s leg, “evidently taking it to be a tree trunk” (p. 83). We can, however, expand this category to include those cases in which animals appear to ignore humans and just continue to do whatever it is that they are doing. Presumably this can be interpreted as a loss of response through habituation, although there appear to be no systematic studies of the process of habituation to people in zoo animals. For the rest of this discussion, I refer to this category as “irrelevant part of the environment.”

Humans as a Member of the Same Species

Hediger (1970) gave a number of examples of incidents that he regarded as indicating that the animals perceived humans as conspecifics. These examples fall into three broad categories. The first category was animals perceiving the human to be a sexual rival or a competitor for dominance and thus showing extreme aggression toward them. His examples of this include deer becoming more aggressive toward keepers when they have their antlers and lions attacking keepers when lionesses are in heat. The second category was animals perceiving their keepers to be potential sexual partners and trying to mate with them. The third category was a longer term process that he referred to as “assimilation”; increasing familiarity with people leads the animals to lose some of their fear, resulting in the human becoming “accepted as a member of their own species with all that this entails with regard to . . . greeting ceremonies, fights between rivals and attempts at mating” (Hediger, 1970, p. 86).

The first two categories were seen by Hediger as being due to inappropriate imprinting, and the third was seen as a longer process of familiarization, although the behavioral outcome could clearly be the same in either case. Other writers at the time gave similar examples. Meyer-Holzapfel (1968), for instance, mentioned parrots and pigeons performing courtship displays only toward humans, but she also mentioned animals having other inappropriate, nonhuman sexual targets, such as a brown hyena attempting to copulate with a water bowl and a chimpanzee and a gorilla behaving sexually toward a cat and a dog, respectively. Similarly, Morris (1964), who called the process “mal-imprinting,” described several hand-reared animals (tiger, marsh mongoose, chimpanzee, and wolf).
who responded to conspecifics with aggression or fear or simply ignored them (pp. 114–117).

Our current views of imprinting have moved on from the classical view that was prevalent when these authors were writing (Hogan & Bolhuis, 2005). In any case, Hediger, Meyer-Holzapfel, and Morris all considered their examples cases of abnormal behavior due to isolation from mothers and/or conspecifics after birth, and we can also regard them in this way. Hediger’s concept of assimilation is of more interest to us; it occurs when animals gradually lose much of their fear of humans and, in his view, come to regard humans (or perhaps particular humans) as conspecifics.

Do these animals really see us as members of the same species? Our only clues are in their behaviors, and Hediger (1970) regarded the animals’ use of species-specific signals to communicate with humans as evidence that they had come to regard us as conspecifics. In one sense, of course, these are the only signals the animals have at their disposal, so we would expect to see them being used regardless of our relationship with that animal. I find it difficult to believe that my cats think I am a cat, or conversely, that they are humans, and they are perfectly capable of communicating with me and with other cats.

Furthermore, assumptions that the use of these signals means that the animals view us as conspecifics are not supported by research on animals’ perceptions of others. Primates, for example, may categorize their conspecifics in several ways, including friends (Cords, 2002; Smuts, 1985). These categorizations may be subtle: De Waal, Dindo, Freeman, and Hall (2005) found that the responses of brown capuchins to a mirror suggested that they did not perceive the image as a stranger but as somewhere between “other” and “self.” How do they categorize humans? In laboratory studies, rhesus monkeys appear to be able to categorize people because they have a concept of “human” (Schrier & Brady, 1987).

In a different context, Mitchell, Obradovich, Herring, Dowd, and Tromborg (1991) investigated the targets of threats by captive golden-bellied mangabeys. They found that keepers and observers (i.e., familiar researchers) were threatened by adult male mangabeys more than neighboring primates (i.e., other primate species in neighboring enclosures) but less than cagemates, and visitors were threatened the most. Mitchell, Obradovich, et al.’s (1991) conclusion was that keepers were treated like familiar conspecifics, observers were treated like familiar neighbors, and visitors were treated like interlopers. Clearly, the mangabeys can put people into different categories according to their familiarity, and they perceive all of them differently from the way they perceive their cagemates.

So, our limited evidence suggests that animals may have more of an ability to classify other animals and humans in more different categories than we previously believed. Sometimes they do perceive us as conspecifics, but in light of the evidence for categorization, I prefer to provisionally regard animals’ views of us as being of either familiar or unfamiliar others.
How Do Animals Perceive Us? The Empirical Evidence

We can treat the three categories postulated by Hediger (1970) as hypotheses and test them against the empirical literature. There are now more than 50 published studies of visitor effects on zoo animals covering a range of species (although predominantly primates) and using a variety of measures both for visitor number and behavior and for animal response. To test our hypotheses against this literature, we need to first predict what sorts of behaviors we would expect to see in animals in each of these categories when faced with humans, and this has been done in Table 1.

Broadly, for animals who see us as enemies, we would expect to see alertness, visual scanning, hiding, and possibly alarm behavior and aggression. Those who treat us as irrelevant parts of the environment should show little or no response at all. Those who view us as conspecifics (or some similar category) might be expected to show approach and possibly affiliative behavior or threats similar to those shown in dominance or territorial encounters. These behavioral responses, of course, should be seen as just a guide to interpreting behavior rather than a definitive list, and we would expect some blurring of the boundaries between them.

Visual scanning could, for instance, also be a response to the approach of an unfamiliar conspecific, and intraspecific and interspecific threats may not be easily distinguishable by us. Many of the published studies did not use these behaviors in their analyses and have therefore been excluded from consideration here. The remaining studies, which include one or more human-directed behaviors among their measures, are summarized in Table 2.

### Table 1

**Predicted Behaviors Expected From Nonhuman Zoo Animals**

<table>
<thead>
<tr>
<th>1. Animal sees us as an enemy</th>
</tr>
</thead>
<tbody>
<tr>
<td>● Human-directed aggression likely to be defensive/high-intensity threat or outright aggression</td>
</tr>
<tr>
<td>● Withdrawing to cover (i.e., hiding)</td>
</tr>
<tr>
<td>● Flight behavior (going to farthest part of enclosure)</td>
</tr>
<tr>
<td>● Alarm calls or behavior</td>
</tr>
<tr>
<td>● High vigilance levels</td>
</tr>
<tr>
<td>2. Animal sees us as part of the inanimate environment</td>
</tr>
<tr>
<td>● Ignore (i.e., humans have no effect on behavior)</td>
</tr>
<tr>
<td>● Uses person as a substrate</td>
</tr>
<tr>
<td>3. Animal sees us as a member of his or her own species</td>
</tr>
<tr>
<td>● Human-directed aggression likely to be offensive/defensive (possibly low-intensity) threat signals and/or dominance/subordinancy/territorial signals and postures</td>
</tr>
<tr>
<td>● Human-directed affiliative behavior</td>
</tr>
<tr>
<td>● Approach</td>
</tr>
<tr>
<td>Species</td>
</tr>
<tr>
<td>---------</td>
</tr>
<tr>
<td><strong>Ungulates</strong></td>
</tr>
<tr>
<td>Fallow deer <em>Dama dama</em></td>
</tr>
<tr>
<td>African pigmy goat <em>Capra hircus</em></td>
</tr>
<tr>
<td>Romanov sheep <em>Ovis aries</em></td>
</tr>
<tr>
<td>Soemmerring’s gazelle <em>Gazella soemmerringi</em></td>
</tr>
<tr>
<td>12 antelope species</td>
</tr>
<tr>
<td><strong>Rodents</strong></td>
</tr>
<tr>
<td>Souslik <em>Spermophilus citellus</em></td>
</tr>
<tr>
<td><strong>Carnivores</strong></td>
</tr>
<tr>
<td>Wolf <em>Canis lupus</em></td>
</tr>
<tr>
<td>6 felid species</td>
</tr>
<tr>
<td>Cheetah <em>Acinonyx jubatus</em></td>
</tr>
<tr>
<td>Jaguar <em>Panthera onca</em></td>
</tr>
<tr>
<td><strong>Primates</strong></td>
</tr>
<tr>
<td>Pied tamarin <em>Saguinus bicolor</em></td>
</tr>
<tr>
<td>Squirrel monkey <em>Saimiri boliviensis</em></td>
</tr>
<tr>
<td>Golden-bellied mangabey <em>Cercocebus galeritus chrysogaster</em></td>
</tr>
<tr>
<td>Mandrill <em>Mandrillus sphinx</em></td>
</tr>
<tr>
<td>Hamadryas baboon <em>Papio hamadryas</em></td>
</tr>
<tr>
<td>Black-and-white colobus <em>Colobus guereza</em></td>
</tr>
</tbody>
</table>

(continued)
<table>
<thead>
<tr>
<th>Species</th>
<th>Behaviors</th>
<th>Reference</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primates</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green monkey C. aethiops sabauea</td>
<td>Spend more time close to visitors and eating visitor-supplied food on public days.</td>
<td>Fa, 1989</td>
<td>Source of stimulation</td>
</tr>
<tr>
<td>Lion-tailed macaque Macaca silenus</td>
<td>Begging from visitors and keepers; more time at front of enclosure.</td>
<td>Mallapur et al., 2005</td>
<td>Source of stimulation</td>
</tr>
<tr>
<td>Siamang H. syndactylus/White-cheeked gibbon H. leucogenys</td>
<td>More time farther from public and out of sight during high visitor attendance.</td>
<td>Smith &amp; Kuhar, 2010</td>
<td>Enemy, but partial habituation</td>
</tr>
<tr>
<td>White-cheeked gibbon H. leucogenys</td>
<td>High levels of interaction with visitors (male) and going out of sight (female).</td>
<td>Lukas et al., 2002</td>
<td>Conspecific through mal-imprinting (male); enemy, but partial habituation (female)</td>
</tr>
<tr>
<td>White-handed gibbon H. lar</td>
<td>Increased looking at visitors.</td>
<td>Cooke &amp; Shillaci, 2007</td>
<td>Enemy, but partial habituation</td>
</tr>
<tr>
<td>Siamand H. syndactylus</td>
<td>Responds to hostile visitor behavior.</td>
<td>Nimon &amp; Dalziel, 1992</td>
<td>Unfamiliar other</td>
</tr>
<tr>
<td>Orangutan Pongo pygmaeus</td>
<td>Look at visitors, hide under sacks.</td>
<td>Birke, 2002</td>
<td>Enemy, but partial habituation</td>
</tr>
<tr>
<td>Orangutan Pongo pygmaeus</td>
<td>Food soliciting but decreased play.</td>
<td>Choo et al., 2011</td>
<td>Source of stimulation</td>
</tr>
<tr>
<td>Gorilla Gorilla gorilla</td>
<td>Increased visual monitoring with increased visitor numbers.</td>
<td>Carder &amp; Semple, 2008</td>
<td>Enemy, but partial habituation</td>
</tr>
<tr>
<td>Gorilla Gorilla gorilla</td>
<td>More frequently not visible when large groups of observers present.</td>
<td>Kuhar, 2008</td>
<td>Enemy, but partial habituation</td>
</tr>
<tr>
<td>Gorilla Gorilla gorilla</td>
<td>Turning back toward glass, more hide and avoid.</td>
<td>Keane, 2005</td>
<td>Enemy, but partial habituation</td>
</tr>
<tr>
<td>Gorilla Gorilla gorilla</td>
<td>Monitored behaviors not affected.</td>
<td>Carder &amp; Semple, 2008</td>
<td>Irrelevant part of environment</td>
</tr>
<tr>
<td>Gorilla Gorilla gorilla</td>
<td>Staring, posturing, and charging at visitors.</td>
<td>Clark et al., 2012</td>
<td>Unfamiliar other</td>
</tr>
<tr>
<td>Gorilla Gorilla gorilla graueri</td>
<td>Monitored behaviors not affected.</td>
<td>Vrancken et al., 1990</td>
<td>Irrelevant part of environment</td>
</tr>
<tr>
<td>Gorilla Gorilla gorilla graueri</td>
<td>One gorilla maintained proximity to public.</td>
<td>Vrancken et al., 1990</td>
<td>Conspecific through mal-imprinting</td>
</tr>
<tr>
<td>Chimpanzee Pan troglodytes</td>
<td>Increased interaction with visitors with increasing visitor number.</td>
<td>Stevens et al., 2008</td>
<td>Unfamiliar other</td>
</tr>
<tr>
<td>Chimpanzee Pan troglodytes</td>
<td>Eye contact, moving closer, and begging.</td>
<td>Cook &amp; Hosey, 1995</td>
<td>Source of stimulation</td>
</tr>
<tr>
<td>Chimpanzee Pan troglodytes</td>
<td>Visitor-directed aggression.</td>
<td>Perret et al., 1995</td>
<td>Unfamiliar other</td>
</tr>
<tr>
<td>Chimpanzee Pan troglodytes</td>
<td>Throwing stones at visitors.</td>
<td>Osvald, 2009</td>
<td>Source of stimulation</td>
</tr>
</tbody>
</table>

Note. The interpretations are provisional, based on discussion in the text and categories illustrated in Figure 1. In particular, behavior directed at humans was interpreted as indicating “unfamiliar other,” whereas visual monitoring or hiding were interpreted as people being seen as “enemies.”
The species here have been grouped taxonomically, as it is possible that the fear of humans, the starting point for animal perceptions of us, differs across different species (Carlstead, 2009; Hosey, 2008). There are also a small number of studies in which there was no change in the measured behavior when people were present, and these are included in Table 2.

Considering the ungulates first, the most commonly observed behavioral response to people in the studies listed is alertness or vigilance. Because vigilance toward humans is also seen in park and wild ungulates (Li, Jiang, Tang, & Zeng, 2007; Shen-Jin et al., 2010; Taylor & Knight, 2003), it is tempting to view this as a straightforward antipredator response, indicating the animals’ view of humans as enemies. The detailed study by Thompson (1989), however, shows that, for zoo ungulates at least, it is more complicated than this. In her study, which observed 12 different species, the animals showed high levels of vigilance toward an unfamiliar keeper, particularly when she was inside the enclosure, but this was not accompanied by eliminative behavior, suggesting the animals were not experiencing stress.

Similar levels of vigilance were shown by the antelope toward other species who shared the enclosure, but vigilance toward zoo visitors was low. There were significant differences in vigilance between species, and larger species showed more vigilance than smaller species, although this result only really held for females and depended on who the target of the vigilance was. Thompson (1989) discounted antipredator behavior and feeding anticipation as explanations but considered that curiosity, resulting in disruption of the spatial cohesiveness of the group, was the best way of accounting for the animals’ responses both to keepers and the public. For our purposes, this implies that ungulates can become less fearful of people in the zoo and can also distinguish the public from keepers, even unfamiliar ones. In addition, the souslik *Spermophilus citellus* study (Górecki, Juszkiewicz, Graclik, & Kala, 2012) appears to also show some habituation to the public in this rodent.

Turning our attention to carnivore studies, the wolves in the study by Beye, Overmeire, and Vervaecke (2007) appeared to show a profile of alertness similar to the ungulates. As with the ungulates, the response to an individual human in an unexpected location, and perhaps showing unusual behaviors, was more pronounced. The jaguar in Sellinger and Ha’s (2005) study spent more time out of sight as visitor numbers increased. But we also have two studies in which the cats appear to show no response to humans at all. In the case of the cheetahs (O’Donovan, Hindle, McKeown, & O’Donovan, 1993), there was no significant difference in either the activity or the spatial location of the cats when the public was present compared with when they were absent. However, these authors did observe 23 responses of the animals to people, and 74% of these occurred when people came inside the boundary rail. They also noted that if a keeper approached the boundary rail, an adult female cheetah charged and displayed interspecific threats.
The study by Margulis, Hoyos, and Anderson (2003) is even more puzzling. They observed six different felid species and looked for changes in active (forage, locomote, affiliative, vocalize, and fight) and inactive (sleep, alert, self-groom, and out-of-view) behaviors under different conditions of visitor presence. They found no significant differences in activity for any of the species when visitors were present compared with when they were absent. It is tempting to conclude that felids are able to treat people as part of the inanimate environment.

However, other studies, which have shown differences in behavior (leopards: Mallapur & Chelan, 2002; jaguars: Sellinger & Ha, 2005) and in cortisol levels (clouded leopards: Wielebnowski, Fletchall, Carlsted, Busso, & Brown, 2002; jaguars: Montanha, Silva, & Boere, 2009), suggest otherwise. Perhaps felids do habituate to humans more readily than ungulates, or perhaps they are more able to conceal behavioral responses to people. In any case, despite these studies we can come to the same conclusion for felids as for ungulates and wolves, which is that they can become less fearful of people in the zoo, that they respond more to people in unexpected places, and that they can distinguish keepers from the public.

When we consider the primates, we have a rather larger set of studies to interpret. Two of the animals in these studies, a female gorilla (Vrancken, Van Elsacker, & Verheyen, 1990) and a male white-cheeked gibbon (Lukas et al., 2002) were hand-reared, and their solicitation of contact and interactions with people may be explained in terms of the imprinting described earlier. For the rest of the animals in these studies, three apparent patterns are discernible: (a) vigilance and looking at zoo visitors and attempts to avoid or hide (gibbons: Cooke & Shillaci, 2007; Lukas et al., 2002; Smith & Kuhar, 2010; orangutans: Birke, 2002; gorillas: Carder & Semple, 2008; Keane, 2005; Kuhar, 2008); (b) aggression toward visitors, sometimes accompanied by movement toward the front of the enclosure (tamarins: Wormell, Brayshaw, Price, & Herron, 1996; mangabeys: Mitchell, Herring, & Obradovich, 1992; Mitchell, Obradovich, et al., 1991; mandrills: Chamove, Hosey, & Schuetz, 1988; hamadryas baboons: Bertolani & Bicca-Marques, 2011; gorillas: Clark et al., 2012; chimpanzees: Perret, Preuschoft, & Preuschoft, 1995); and (c) soliciting food or moving toward the public in order to obtain food (green monkeys: Fa, 1989; macaques: Mallapur, Sinha, & Waran, 2005; orangutans: Choo, Todd, & Li, 2011; chimpanzees: Cook & Hosey, 1995; Wood, 1998).

In the first case (vigilance, avoid and hide), the animals appear to be behaving in a manner similar to the ungulates and carnivores, implying again that they are fearful of humans but that fear can diminish within the zoo. That process of reduction of fear can presumably occur simply through habituation, which would suggest that for those animals the majority of their interactions with people have no great negative or positive consequences. Reinforcement of animal proximity and interaction by the public in the form of food (even if it is not permitted
by the zoo) would lead to a different sort of relationship between visitors and animals, and this is perhaps what we are seeing in the green monkeys, lion-tailed macaques, orangutans, and chimpanzees identified earlier.

In the case of aggressive interactions with visitors, it is instructive to look more closely at the housing of the animals involved. In Wormell et al.’s (1996) study, two separate groups of tamarins showed aggressive behaviors toward the public, but by far the most threats (7.63 per animal per hour) were shown by a group in an enclosure with a high visitor number, with markedly less (0.06 per animal per hour) in the second group in which visitor attendance was lower. The authors interpreted this aggression as territorial defense.

The mangabeys in the series of studies by Mitchell and colleagues (Mitchell, Herring, et al., 1992; Mitchell, Herring, et al., 1991; Mitchell, Herring, Tromborg, et al., 1992; Mitchell, Obradovich, et al., 1991; Mitchell et al., 1990) showed a similar pattern. Out of three groups housed in separate enclosures, the group showing the most aggression toward visitors was in the enclosure with the highest number of visitors. When animals were moved to the enclosure with higher visitor attendance, they showed an increase in their visitor-directed aggression. Similarly, moving animals to an enclosure with lower visitor pressure resulted in a reduction of visitor-directed aggression.

As mentioned previously, the number of threats to humans and nonhuman primates were significantly different: visitors > cagemates > keepers and observers > neighboring primates. It was intriguing that male humans and mangabeys threatened each other, and female mangabeys and female humans threatened each other as well. Mitchell, Herring, Tromborg, et al. (1992) concluded that the mangabeys respond to zoo visitors as they would to strangers of their own species, and they suggested that the underlying motivation was about competition for resources. Keepers and observers (i.e., familiar people), however, are clearly seen in a different category, as are neighboring primates of other species.

All of these studies appear to show that (a) animals have a natural fear, or at least wariness, of people and that the magnitude of this fear may differ in different species (in Hediger’s terms, they see us as enemies); (b) this fear may be reduced through increased contact with people, either because that contact has no negative consequences (the animals habituate to human presence, and in Hediger’s terms, come to regard us as part of the inanimate environment) or because it has positive consequences, either because humans become a source of stimulation even if they are unfamiliar or because they become familiar and a positive relationship can develop (in Hediger’s terms, they see us as members of the same species, but we can more properly think of them perceiving us as familiar others, which may be as familiar conspecifics or as familiar heterospecifics); (c) the fear may be increased through increased contact with people if that contact has negative consequences for the animal (they still see us as enemies); and (d) many (most?) animals can discriminate between different
Assuming that animals in zoos initially have a basic fear of humans, then subsequent interactions with people can perhaps change that fear in the ways shown, depending upon the quality of those interactions.

All of the papers reviewed here appear to fit this general interpretation. They also permit us to suggest two further ways in which captive animals might perceive people who are familiar and unfamiliar others: as a source of stimulation in the environment or as a friend.

Humans as a Source of Stimulation

In several of the studies listed in Table 2, the animals did not behave toward people as if they were enemies or familiar conspecifics/heterospecifics. The chimpanzees at Chester Zoo, for example, were willing to sustain quite long sequences of interactions with the public, sequences that often culminated in the animals begging for food (Cook & Hosey, 1995). Similarly, the behaviors of the green monkeys at Mexico City Zoo appeared to be primarily about soliciting...

FIGURE 1 Assuming that animals in zoos initially have a basic fear of humans, then subsequent interactions with people can perhaps change that fear in the ways shown, depending upon the quality of those interactions.
food from visitors (Fa, 1989). Morris (1964) discussed at some length cases in which zoo animals appear to use zoo visitors as a source of stimulation. Morris pointed out that begging was unlikely to be motivated by hunger and viewed it as evidence of the animals “craving novel social interaction” (pp. 103–104).

Morris (1964) gave examples of other interaction-seeking behaviors, such as animals enticing visitors with a friendly invitation to groom and then biting or pecking them, animals directing urine or feces at visitors, and animals banging and stamping on the ground to attract an audience. A more recent example involves chimpanzees throwing stones at zoo visitors (Osvath, 2009), which can possibly be interpreted as seeking stimulation rather than as aggression to a perceived enemy because in this case the animals collected stones in anticipation of using them later. In Morris’s view, interactions between humans and animals in the zoo provided the animals with a source of environmental variability, in essence helping to relieve the animals’ boredom.

Morris (1964) was writing at a time when most zoo enclosures were very barren in comparison with modern standards, and if some interactions are about increasing environmental variability, then we might expect them to occur less frequently in the modern zoo. Unfortunately, we have no data on this, and little research appears to have been undertaken on the motivation of begging and similar behaviors. In Asian small-clawed otters Aonyx cinereus, an hourly provision of mealworms and crickets led to a reduction in the animals’ begging behaviors, especially when the food allowance was increased (Gothard, 2007), suggesting that the motivation of begging might be related to food after all.

But the provision of food in this way simulates otter feeding ecology better than one or two main feedings, so boredom reduction cannot be discounted either. Similarly, bears who beg show fewer stereotypies than animals who do not beg (Van Keulen-Kromhout, 1978), again suggesting that begging might replace some other appetitive behavior. So, it appears that some animals in zoos may sometimes see unfamiliar people simply as a source of stimulation.

**Humans as Friends**

Animals who live in social groups do not behave in the same way toward all of their group members. Some dyads show greater frequencies of affiliative behaviors than others and spend more time in close proximity. In the primate literature at least, these are often called “friendships” (e.g., Cords, 2002; Smuts, 1985) if they involve nonkin dyads, and research has concentrated on the functional benefits that such relationships might confer. Recently, it has been argued that these animal friendships, which have conventionally been regarded as conditional, are in fact equivalent to human friendships even though the latter are usually thought of as unconditional (Massen, Sterck, & de Vos, 2010). Whether such friendships can occur between species is a lot less clear.
The evidence is inevitably mostly anecdotal, but a surprising number of instances of apparent interspecies friendships have been reported (Dagg, 2011). Can friendships be formed between human and nonhuman animals? We characteristically view our relationships with our companion animals as friendships (Beck & Madresh, 2008; McConnell, Brown, Shoda, Stayton, & Martin, 2011; Peretti, 1990; Serpell, 1986), although this perception is from the human side of the relationship (Shore, Douglas, & Riley, 2005). Dagg (2011) gives further examples of human friendships with a range of animals, including chimpanzees, wolves, horses, parrots, and whales. But again, as Dagg points out, friendship is just the human way of seeing the relationship. Determining whether an animal sees it in quite the same way is another thing entirely.

For our purposes, we can think of a friendship as being a particularly good relationship, the product of a history of mostly positive interactions between two individuals. In this respect, a friendship can effectively be regarded as a bond between those two individuals, and in principle it can be measured through behaviors such as affiliation, grooming, seeking proximity to each other, and spending time in close contact. People who work with animals in the laboratory have been aware that they have what they believe to be bonds with some of the animals (Bayne, 2002; Davis & Balfour, 1992; Russow, 2002), and the behaviors of the animals appear to indicate that the bonds are indeed reciprocal (Rennie & Buchanan-Smith, 2006).

There is evidence that many zoo professionals also believe that they have bonds with some of the animals (Hosey & Melfi, 2012), although here again the perception of a friendship is from the human perspective. Observational evidence of changes in animal behavior is needed to demonstrate the reality of human-animal friendships, but certainly the anecdotal evidence (e.g., Dorfman, 2005; Martin, 2004) suggests that this is another way in which animals in zoos might see us.

ANIMAL WELFARE IMPLICATIONS

In order to achieve their conservation and education goals, zoos need to attract visitors and provide them with an enjoyable experience, and that means that the animals must spend a lot of their time in close proximity to people (Fernandez, Tamborski, Pickens, & Timberlake, 2009). It is important for us to know if this contact has any impact on the welfare of the animals, and if so, whether any deleterious effects can be ameliorated or even whether human contact could potentially be turned into a source of enrichment for the animals (Claxton, 2011). There is a substantial body of evidence that the presence of people in zoos can result in changes in the animals’ behaviors (Davey, 2007; Hosey, 2000, 2005, 2008; Fernandez et al., 2009). Whether these changes in behavior...
indicate a reduction in the animals’ welfare is less clear, partly because there are inconsistencies in the way behavior changes both across species and within species.

Although some of these inconsistencies result from the use of different measures and differences in the housing of animals, it has also been suggested that quality of the previous contacts that individual animals have had with people leads them to respond in their own individual ways. Effectively, animals in zoos establish relationships (which might be good, neutral, or poor) with their keepers and perhaps also establish generalized relationships with unfamiliar people (i.e., zoo visitors), which might also be good, neutral, or poor (Hosey, 2008). In other words, individual animals perceive individual people and groups of people in particular ways according to the histories of interactions they have had with those people or with similar groups in the past.

If the interpretations of this analysis are correct, then it appears that animal perceptions of people in zoos can change in the ways indicated in Figure 1; the animal sees people or groups of people as enemies; as irrelevant parts of the environment; or as either familiar or unfamiliar conspecifics or heterospecifics, some of which are seen as just a source of stimulation in the environment whereas others are seen as friends. Each of these perceptions might be appropriate in certain circumstances. Animals destined for reintroduction to the wild, for example, should perhaps view people as enemies. But for animals who are going to spend their whole lives in the zoo and be in contact with people during that time, reducing the animals’ fear of humans and gradually replacing it with a perception of people as familiar others, maybe even as friends, could help ensure their best welfare. For this to be the case, we would need to be satisfied that positive interactions with people really do have welfare benefits.

Zoos have limited influence over the quality of interactions that animals have with the public but can use signage and educational events to try to improve public behavior toward the animals (Kratochvil & Schwammer, 1997; Visscher, Snider, & Stoep, 2009). They can, however, influence the quality and quantity of interactions that the animals have with keepers. If very good relationships (perhaps even friendships or bonds) can be established between keepers and individual animals, then the hope would be that they would help the animals to perceive unfamiliar people (such as zoo visitors) more positively and perhaps be less adversely affected by their presence and their behavior. Figure 2 shows a model to illustrate why this might happen; it is derived from a more preliminary model published previously (Hosey, 2008) and is ultimately based on a model developed for agricultural animals by Hemsworth (2003).

The perceptions of humans by animals and of animals by humans are determined by their attitudes toward each other, ranging from fear to affection. These attitudes can be reinforced or changed through the interactions they have with each other, and as a result, their perceptions of each other can change.
FIGURE 2 Model to illustrate how human and animal perceptions of each other may be modified through their interactions. Animal perceptions of people (whether they are hostile or friendly) are influenced by their “attitudes” (which are in turn influenced by factors such as their species, personality, and how much control they have over encounters with humans) and also by the net quality of interactions they have with people. Human attitudes likewise influence the ways they perceive and behave toward animals. The animals’ responses to human interactions can change people’s perceptions of them, and hence their attitudes and behaviors toward them, just as human responses to animals can affect their perceptions and hence future behaviors toward people (color figure available online).

Other factors, such as species, personality, and the amount of control the animal has over his or her encounters with people, also affect the animal’s attitudes, and there is no doubt that there are other influences on human attitudes toward animals as well.

So, if an animal is initially fearful of humans, then regular, positive interactions with keepers (e.g., the keepers talking to the animal and providing food) may result in the animal having the perception that those humans are friendly, and the animal’s attitudes would then move from fear toward indifference or even liking. Behaviors toward people, including unfamiliar people, may then move from negative to neutral or even positive, which would then lead people to perceive that the animal is friendly, thus affecting their attitudes and behaviors toward the animal. That is clearly a very simplified, indeed optimistic, account
of the development of this system, but there is some support from the empirical literature.

There is evidence from animals in a number of contexts that human contact can have a positive effect on behaviors. For example, rats will lever-press when human contact is the reward (Davis & Pérusse, 1988); stroking dogs reduces their heart rates, blood cortisol levels, and behavioral indicators of stress (Wells, 2004); and dolphins who have taken part in shows or interactive programs show increases in positive behaviors (Miller, Mellen, Greer, & Kuczaj, 2011; Trone, Kuczaj, & Solangi, 2005). Simply increasing the time keepers spend with the animals can lead to less abnormal behavior and inactivity and greater grooming of other animals in chimpanzees (Baker, 2004) and to increased grooming and play in marmosets (Manciocco, Chiarotti, & Vitale, 2009).

The increased human contact that comes from structured activities such as positive reinforcement training (PRT) can also have positive effects on animal behavior and interactions with people (McKinley, Buchanan-Smith, Bassett, & Morris, 2003; Savastano, Hanson, & McCann, 2003). Positive interactions with people can affect animals’ behaviors in what appears to be a positive way, which can increase the positivity of their interactions with people.

Can positive interactions with keepers result in animals reducing their fear of unfamiliar people? In terms of the changes shown in Figure 1, this would require helping animals to move from perceiving unfamiliar people as enemies to their perceiving these people as irrelevant parts of the environment or even as familiar heterospecifics. Again, there is some evidence that this works. After undergoing PRT to achieve oral examinations, Abyssinian colobus monkeys reduced their interactions with members of the public (Melfi & Thomas, 2005); increasing feeding enrichment of several monkey species increased the likelihood that they would accept food from a stranger (Baker & Springer, 2006); and PRT and play therapy with gorillas led to a decrease in the animals’ interactions with the public, stereotypies, and other undesirable behaviors and an increase in affiliative and play behaviors (Carrasco et al., 2009).

The literature then suggests that this is a worthwhile avenue to pursue, and further empirical studies are (as always) needed to test the general conclusions of this analysis and the detailed features of the processes proposed. How could zoos make use of this information? Different individual animals have different roles within the zoo, and an appropriate first step would be to identify what perception of humans would be most compatible with each particular role.

But a major concern for most zoos is the possibility of long-term exposure to the public being a source of chronic stress for the animals. Signage, education, camouflage barriers, and hiding places all help to reduce this possibility, but what is being suggested here is that additional positive contact with keepers (and maybe with the public too, although this is perhaps more controversial) could help animals perceive both their keepers and the public in the most favorable
light if it is compatible with the roles those animals have in the zoos. It would be very encouraging if positive relationships between animals and their keepers really did have wide-ranging welfare benefits across the whole spectrum of mammalian species in zoos.

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REFERENCES


HOSEY


