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Sources of stress in captivity[☆]

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Abstract

Animals housed in artificial habitats are confronted by a wide range of potentially provocative environmental challenges. In this article, we review many of the potential stressors that may adversely affect animals living in captivity. These include abiotic, environmental sources of stress such as artificial lighting, exposure to loud or aversive sound, arousing odors, and uncomfortable temperatures or substrates. In addition, confinement-specific stressors such as restricted movement, reduced retreat space, forced proximity to humans, reduced feeding opportunities, maintenance in abnormal social groups, and other restrictions of behavioral opportunity are considered. Research in support of the claims for these environmental elements as stressors for captive animals reveals no unique suite of behavioral or physiological responses that will clearly indicate the cause of those responses; rather, it is up to us as managers and caretakers of animals in captivity to evaluate enclosures and husbandry practices to ensure the optimal well-being of animals in our care.

1. Introduction

The myriad species with which humans cohabitate are equipped with physiological and psychological mechanisms for adapting to various levels of challenge from their surroundings. Among these adaptive mechanisms is a suite of behavioral and physiological responses to stress. The word ''stress'' has become used in so many different contexts that it has been argued by some to be an essentially useless term (McEwen, 2000). Nonetheless, the general understanding of the

term in common parlance necessitates its continued use, and we will employ the term "stress" and related terms throughout this paper as follows.

For the purposes of this document, stress will be defined as the experience of having intrinsic or extrinsic demands that exceed an individual's resources for responding to those demands (Dantzer, 1991). Living systems have evolved to reduce these demands and maintain the status quo through a series of physiological and sometimes behavioral responses. The tendency of systems to maintain a steady state is referred to as homeostasis, and for some authors a "stressor" is anything that challenges homeostasis (e.g., Michelson et al., 1995; Selye, 1976). For the most part, this is the definition of "stressor" that we will use throughout this paper. A "stressor" in this case may be an actual physical challenge to homeostasis (such as exposure to a sudden change in temperature, physical restraint or combat), or the threat of such a challenge (such as a direct stare from a more dominant individual, or the approach of a human with handling gloves). In either case, stressors result in a cascade of physiological events designed to prepare the body for homeostatic challenge—the so-called "fight or flight" response.

In general, the "fight or flight" response involves increased autonomic activity and shifts in the metabolic profile of an organism as it adjusts to some perceived threat from its surroundings. Acute, short-term stressors are typically associated with behavioral responses of orientation, alarm, and increased vigilance. Physiological components of this response profile include tachycardia, increased respiration rate, increased glucose metabolism, and an increase in various isomers of glucocorticoids (GCCs), which shift metabolism toward energy mobilization and away from energy conservation. In comparison, chronic, long-term stress results in prolonged elevation of GCC levels that in effect become self-sustaining, as prolonged high levels of circulating GCCs damage areas of the brain responsible for terminating the stress response (for a review of this mechanism, see Sapolsky and Plotsky, 1990). Physiologically, chronic stress may be indicated by suppressed reproductive cycling (Chrousos, 1997), blunted activation of the HPA (hypothalamic-pituitary-adrenal axis) response to acute stress (Goliszek et al., 1996), suppressed immune responses (Barnett et al., 1992; Ferrante et al., 1998), reduced growth hormone levels and subsequently inhibited growth rate (Chrousos, 1997; Tsigos and Chrousos, 1995), and reduced body weight (Bartolomucci et al., 2004; Konkle et al., 2003). Behaviorally, chronic stress may be indicated by reduced reproductive behavior (Gronli et al., 2005; Hemsworth et al., 1986a), increased abnormal behavior (Carlstead and Brown, 2005; Schouten and Wiegant, 1997), reduced exploratory behavior and increased behavioral inhibition (Carlstead and Brown, 2005; Carlstead et al., 1993b; Vyas and Chattaji, 2004), increased vigilance behavior and increased hiding (Carlstead et al., 1993b), reduced behavioral complexity (Rutherford et al., 2004), increased aggression (Bartolomucci et al., 2004; Mineur et al., 2003), increased fearfulness and frequency of startle (Boissy et al., 2001), and increased freezing behavior and decreased latency to freeze (Korte, 2001). All of these physiological and behavioral measures have been used to operationally define chronic stress in captive animals, as can be seen in the literature review below. For the purposes of this article, we will consider a given behavior to be an indication of chronic stress if the authors of a given publication consider it to be so, and substantiate their position with appropriate literature.

While acute stress responses can be considered adaptive, enabling animals to escape from danger, chronic stress responses are fraught with danger to the long-term health of captive animals (Broom and Johnson, 1993; Sapolsky, 1996; Sapolsky et al., 1990). Occasional exposure of captive animals to environmental provocation might be considered as legitimate components of long-term husbandry regimes (Chamove and Moodie, 1990; Moodie and Chamove, 1990), particularly for those species targeted for eventual repatriation (McLean et al., 2000; Rabin, 2003). But relentless exposure to persistent stressors can have many deleterious consequences

that are particularly undesirable for animals maintained in captivity, including increased abnormal behavior (Capitanio, 1986), increased self-injurious behavior (Bellanca and Crockett, 2002; Reinhardt and Rossell, 2001), impaired reproduction (Moore and Jessop, 2003; Tilbrook et al., 2002) and immunosuppression (Kanitz et al., 2004). Even if we were not compelled for humane reasons to reduce stress in our captive populations, the economic impact of adverse environments on captive animals should be sufficient to demand our attention.

One of the putative sources of stress in captivity is interference with or prevention of animals' engagement in species-typical behaviors for which they appear to have a "behavioral need." The concept of behavioral needs is controversial (Cooper, 2004; Hughes and Duncan, 1988; Jensen and Toates, 1993); however, at least some animal welfare legislation assumes such needs exist (Brambell, 1965; Sumpter et al., 1999) and animal care standards have been mandated accordingly. Behavioral needs can be broadly defined as behaviors that appear to be largely internally motivated, since they may occur even in the absence of appropriate trigger stimuli. Such behaviors appear to be those that an animal *must* perform, regardless of environmental conditions (Mench, 1998), and preventing animals from performing such behaviors is thought to be detrimental to their well being (Friend, 1989). It is not in the purview of this article to discuss the concept of behavioral needs (for a review, see Dawkins, 1990); however, some researchers investigating sources of stress in captivity describe behavioral deprivations in terms of behavioral needs. When a given author uses this term in his or her work to describe results, we will also use the term in such a way.

Perhaps the greatest stressor in populations of captive animals are those over which the animal has no control and from which they cannot escape. In this article, we review many uncontrollable stressors that might confront animals in captivity. Our purpose is to identify and describe these stressors, and to review the literature suggesting that they indeed have adverse effects on captive populations. It is our hope that in so doing, we will provide a functional checklist for evaluation of artificial environments as to their stress potential, so that improvements or alterations may be made as necessary for the benefit of animal well-being.

2. Abiotic environmental stressors: the presence or absence of critical sensory stimuli

Prior to the introduction of the concept of environmental enrichment (Markowitz, 1975), most artificial environments were structurally simple and unresponsive to behavior. Typically, these environments did not provide animals with opportunities to interact with their surroundings in ways which promoted the development of sensory and cognitive abilities, or that allowed display of species-typical behaviors.

Contemporary views of animal welfare have substantially changed the nature of captive environments. Over the past several decades, scientists have developed strategies for improving the conditions of captivity that include means by which to increase animals' behavioral opportunities. Researchers have investigated the effects of modifying the structure, complexity, and interactivity of traditional and artificial environments on the behavior and health of captive animals (e.g., Baumans, 2005; Markowitz, 1982; Markowitz and Spinelli, 1986; Shepherdson et al., 1998).

Contemporary methods for improving artificial environments include, but are not limited to, enhancing several abiotic parameters, such as increasing natural sound and improving substrate complexity (Carlstead et al., 1993a; Lutz and Novak, 1995; Sneddon and Beattie, 1995). Elements from natural habitats have been introduced into zoo exhibits, imbuing them with an apparent naturalism for visitors and enhancing their ecological relevance to captive animals (Hutchins et al., 1984). More complex, enriched environments offer animals greater

opportunities for exploration and withdrawal from observation. Increased behavioral options allow animals to respond to adverse environmental conditions by managing confinement-related stress (Carlstead et al., 1993a).

Finally, in some instances, interactive or automated technologies have been employed to increase opportunities for animals to engage in complex problem solving while contending with variation in the physical properties of their environments (Markowitz, 1982). In essence, intelligently managed zoological gardens attempt to preserve species-typical behavior (Markowitz, 1997; Rabin, 2003).

While many of these environmental enrichment strategies have undoubtedly improved the conditions of captivity (Bloomsmith and Else, 2005; Kuehn, 2002; Sorensen et al., 2004; Swaisgood et al., 2001), they have tended to underemphasize the influence of artificial environments on the sensory behavior of captive animals. In some cases this apparent neglect may be due to constraints imposed by the finances or structure of the facilities in which animals are housed; in others, the dearth of information on species "umwelt" is to blame. While enrichment techniques in many cases have the aim of improving animals' abilities to cope with the artificial conditions of captivity, the unfortunate truth is that we are often unaware of sensory elements of the captive environment that animals may find stressful. The sensory stimuli of which we humans are aware are limited, and what is "out of sight" for us may inadvertently stay "out of mind" when considering our animal charges.

In contrast to how humans perceive them, the artificial environments typical of captivity are full of sensory stimuli that might be at best alien to an animal, if not overtly stressful. Unnaturally intense, punctate, or constant sound, the odor or sight of historic ecological adversaries, the elimination of scent-marks with daily cage cleaning, the rough and unyielding surfaces of gunite, tile, wire, or concrete, and exposure to aberrant lighting conditions might all be sources of environmental stress for animals in captivity. Below, we review evidence that suggests these factors as sources of stress.

2.1. Sound

Based on the amount of research focusing on audio-vocal behavior in nonhuman animals, one might rightly conclude that the auditory sensory modality is a critical feature of many of their natural histories (Byrne, 1982; Ehret, 1980). Yet much remains unknown about the auditory ranges of most species. This ignorance prevents adequate assessment of auditory risks to animal welfare, since in modern facilities that house animals, relatively high levels of unnatural noises in variable frequencies are routinely produced. Unfortunately, many of the surfaces within these facilities are extremely acoustically reflective (Gamble, 1982; Tromborg, 1993). Recordings of the sound pressure levels (spl) at two Northern California zoological parks (San Francisco and Sacramento) ranged from a low of 62 dB (spl) to a high of 72 dB (spl), with an average of 70 dB (spl), and was influenced by the number of visitors, the intensity of their conversations, the presence of maintenance machinery or exhibit water features, and the amplitude of sounds of surrounding urban transportation systems (Tromborg and Coss, 1995). Ambient sound in laboratories is no better. During cage cleaning, for example, sound pressure levels at a primate research center exceeded 80 dB (spl) (Morgan, personal observation; Peterson, 1980). Sound levels exceeding 90 dB (spl) have been recorded in some laboratories housing rats (Pfaff and Stecker, 1976), and over 110 dB when ventilation equipment was running in others (Sales et al., 1999). In these and similar studies, sound pressure levels correlated with caretaking activity.

These sound levels contrast sharply with sound levels in natural environments. In the wild, ambient noise levels are highest in rain forest habitats, moderate in riverine habitats, and lowest in savannah habitats—but in no case do sound pressure levels in nature approach the levels recorded at zoos or in laboratories. In rain forest habitats, ambient noise levels range from 27 dB at 06:00 to 40 dB at 15:00, largely a consequence of wind and rustling of leaves (Waser and Brown, 1986). In riverine habitats, sound intensities range from 27 dB at 06:00 to 37 dB at 07:00, while in savannah habitats the levels range from 20 dB at 06:00 to 36 dB at mid-day. In riverine habitats, ambient noise arises largely from bird vocalizations, insect stridulations, and rustling vegetation. In savannah habitats, virtually all noise arises from wind.

Many laboratory animals begin to exhibit symptoms correlated with elevated stress when ambient sound pressure levels approach 85 dB (spl) for extended periods of time (Anthony et al., 1959). The typical sound pressure levels measured in zoos and in laboratories are lower than this but still substantially higher than the 20 dB (spl) to 40 dB (spl) characteristic of various natural habitats. Clearly sound pressure levels in captivity exceed those found in the natural environment itself!

Elevated sound pressure levels have been shown to exert deleterious influences on many species of laboratory animals (Gamble, 1982), affecting their behavior in ways that could introduce confounds into behavioral studies. This is especially true when there is an irregular periodicity of sounds of moderate to high intensity. Consider the periodic loud sounds of metal striking metal that may occur in an animal facility during cage cleaning—such sounds are typically full of harmonics in a wide range of frequencies, and can often be extremely loud (in excess of 80 dB (spl); Tromborg and Coss, 1995). Commercial trucks when backing up emit high frequency, punctate sounds in excess of 90 dB (spl) (Tromborg and Coss, 1995). Firework displays – a not uncommon event in city greenspaces that also accommodate zoos – can exceed 120 dB (spl) in short, punctate bursts. Continuous loud sounds may be produced by environmental control systems such as air pumps, air conditioners, and heaters, and by activities such as floor washing and lawn mowing (for a review of sound pressure levels associated with these and other animal maintenance activities, see Sales et al., 1999).

Both constant and periodic sounds can subtly influence the physiology of some particularly sensitive species. Compared with chronic background or repetitive noise, high amplitude punctate, aperiodic, or unpredictable noise is especially effective at provoking distress responses (Cottereau, 1978; Gamble, 1982; Stoskopf, 1983). This type of reactivity is especially evident in easily aroused species, particularly those that are targets of predators in nature (Meyer-Holzapfel, 1968; Stoskopf, 1983).

Animals continuously subjected to intense noise manifest stress responses by exhibiting elevated levels of arousal (Gamble, 1982), both behaviorally and physiologically. Loud sound is well known to have adverse effects on blood pressure and heart rate in humans (Hagerman et al., 2005; Smith, 1991) and other animals (Geverink et al., 1998; Salvetti et al., 2000). Physiologically, prolonged exposure to intense noise is associated with increased activity in the sympathetic division of the autonomic nervous system. Its prolonged activation is correlated with increased activity in the hypothalamic-pituitary-adrenal (HPA) system, elevated metabolic rates, increased blood pressure, and tachycardia (Ames, 1978; Anthony et al., 1959; Henkin and Knigge, 1963). This arousal can have deleterious long-term effects on animals that experience it directly (for a review, see Sapolsky et al., 1987), but also on offspring in utero. Exposure of pregnant animals to noise-induced physiological arousal results in immunosupression (Sobrian et al., 1997), exaggerated distress responses to aversive events (Morgan and Thayer, 1997), changes in auditory threshold (Canlon et al., 2003), increased disturbance behaviors (Schneider

et al., 2002), impaired learning (Nishio et al., 2001; Morgan et al., 1999), abnormal social behavior (Clarke and Schneider, 1993; Morgan et al., 1997), and suppressed exploratory behavior (Poltyrev et al., 1996) in offspring. Such long-term effects of exposure to loud sound are important considerations for conservation-minded managers of animals housed in the typically noisy surroundings of captivity.

Behavior of adult animals in captivity is also affected by noise. In zoos and aquaria, noise from visitors increases as visitor numbers increase, and this correlates with increased vigilance behaviors in harbor seals (Suarez and Morgan, unpublished data), cotton top tamarins (Tromborg, 1993), and orangutans (Birke, 2002). Caretaker sounds result in more frequent clinging to adults by infant gorillas (Ogden et al., 1994), and noise made by humans shouting and metal clanging increases heart rate and activity in cattle (Waynert et al., 1999). Laboratory rabbits alter their behavior in significant ways when exposed to normal laboratory sounds in nonsound isolated housing (Jildge, 1991), including shifting their normal activity patterns from night to day. And noise in rabbitries is associated with abnormal behavior and startle that can result in serious injury (Marai and Rashwan, 2004). Loud sound has been shown to increase vigilance and activity in rats (Krebs et al., 1997) and agitation behaviors in pandas (Owen et al., 2004). In the wild, caribou respond to the sound produced by aircraft flyovers with increased activity, although the degree of reaction varies with time of year (Maier et al., 1998). Similar effects of aircraft noise have been found in captive desert mules and mountain sheep (Bleich et al., 1990; Weisenberger et al., 1996). These data indicate that anthropogenic noise generated in the course of routine human activity may have adverse effects on our nonhuman animal charges.

Sounds other than those produced by humans might also be stressful for captive animals. For prey species, the sound, smell, and sometimes sight of their historical predators may be constant when in captivity. Such sounds may be a continual source of stress. Crows, for example, respond with defensive behaviors to the sound of raptors (Hauser and Caffrey, 1994) as do mice (Hendrie and Neill, 1991), suggesting that the sounds of historical predators are perceived as threating and therefore a potential source of stress. The sound of conspecifics may also be stressful under certain conditions. For example, the sound of chimpanzee screams has been shown to evoke cardiac orienting responses in young chimps (brachycardia associated with increased vigilance and attention), regardless of their early experiences with other chimps (Berntson et al., 1989). At the same time, sound (including music, the sound of prey, and the sound of conspecifics) has been used as an enrichment strategy for some species (e.g., Cloutier et al., 2000; Markowitz et al., 1995; Shepherdson et al., 1989). Thus the impact of different sounds on animals in captivity is by no means unequivocal.

Adding to our difficulty in understanding the potential impact of sound on captive animals is the fact that our own detection of sound is quite limited. In some cases, anthropogenic sound that is stressful to nonhuman animals in captivity may not be detectable by humans. Many devices common in captive environments such as computer monitors, closed circuit security cameras and televisions, and fluorescent lights produce high-frequency sounds (higher than 20 kHz) that despite our inability to hear them are potentially quite loud to animals that detect sound in this range. In one study, 24 out of 39 sources of sound in captive environments included frequencies in excess of 60 kHz (Sales et al., 1988). And in many cases, these sounds may be extremely loud, despite our not being able to hear them. For example, sound pressure levels exceeding 75 dB have been reported at frequencies in excess of 60 kHz in some laboratory animal housing (Milligan et al., 1993).

Ultrasonic sound is produced and detected by a number of species from a variety of taxa, including hummingbirds (Pytte et al., 2004), swiftlets (Fullard et al., 1993), rats (Sanchez, 2003),

mice (D'Amato and Moles, 2001), prairie dogs (Heffner et al., 1994), bats (Griffin et al., 1960), ground squirrels (Wilson and Hare, 2004), some species of fish (Mann et al., 2001), dolphins (Lammers et al., 2003), orca (Szymanski et al., 1999), hamsters (Johnston, 1992), dogs (Lipman and Grassi, 1942), and voles (Blake, 2002). Since it is clear that the ability to detect ultrasound has evolved in a number of different taxa and also that our understanding of comparative perception is limited, it is likely that many other species detect ultrasound. Thus, the potential for stress induced by exposure to anthropogenic ultrasonic sound in captive environments should not be negated.

A number of animals also detect infrasound, including giraffe (von Muggenthaler et al., 1999), elephants (McComb et al., 2003), cassowaries (Mack and Jones, 2003), hippopotamus (Barklow, 1997), pigeons (Quine, 1979), tigers (von Muggenthaler, 2000), chameleons (Barnett et al., 1999), rhinoceros (von Muggenthaler, 1992), alligator (Vliet, 1989), moles (Mason and Narins, 2002), prairie dogs (Heffner et al., 1994), and okapi (Lindsey et al., 1993). Others such as mole rats that spend most of their lives underground are sensitive to seismic vibration at frequencies well below human thresholds (Kimchi and Terkel, 2002). Again, the diversity of species known to respond to sounds below the human threshold for hearing suggest that many other species also detect infrasound, although the auditory ranges of few have been studied. Clearly more needs to be done to describe the auditory profiles of captive species. Because many devices (such as trucks, pumps, filters, and other engines) used in captive environments generate seismic vibration and other infrasonic sound, there is potential for animals sensitive to these sounds to be distressed by them. Additional research is needed to describe the acoustic nature of captive environments (including ambient sounds above and below the range of normal human hearing) and how these sounds might adversely affect captive animals, so that we can develop effective strategies for ameliorating such effects.

2.2. Light conditions

Lighting conditions in captive environments are designed for human convenience, and this presents a host of potential problems for nonhuman animals living in such environments. In some captive settings, light level may be constant or nearly constant. In others, lighting may be varied periodically according to a fixed schedule. In either instance, artificially maintained photoperiodicity generally suits human needs and does not reflect natural light conditions. Photoperiod not withstanding, another feature of lighting in captivity that may adversely affect animal welfare is the intensity and spectral composition of the light. Fluorescent lighting that is favored because of its reduced maintenance costs may also restrict access to particular wavelengths of light needed for optimal animal well-being. Strong contrasts between light and dark areas of an animal's environment may arouse fear (Grandin and Johnson, 2005), as may flicker in fluorescent light bulbs. If animal welfare is to be maximized in captivity, then attention to lighting must be given (Belhorn, 1980; Hediger, 1964).

Traditionally, animals housed in artificial surroundings have been subjected to arbitrary light cycles, commonly 12 h of light alternating with 12 h of dark. On the other hand, constant lighting is a common practice in many agricultural settings (Hester, 1994). Neither of these lighting regimes consider the effect of light cycles on behavior. Constant exposure to extended photoperiods can alter the melatonin to serotonin ratio, affecting the rate of catabolic and anabolic activity of important enzymes in the central nervous system (van Rooijen, 1984). Continuous exposure to light also suppresses circadian activity (Ikeda et al., 2000), and as anyone who has ever experienced jet lag can tell you, disruption of normal circadian rhythms is stressful.

In at least one study, varying light conditions produced differences in sleep behavior in rats (Vanbetteray et al., 1991). Disruptions of sleep and circadian cycles have been used to induce stress in some experiments; thus, if lighting conditions can adversely affect sleep, they have obvious impacts on stress. In mice, the stressful effect of disruptions in light conditions is quite apparent, resulting in increased levels of plasma corticosterone and reduced latencies for aggression (van der Meer et al., 2004). In chickens too, continuous lighting is associated with CBC levels indicative of stress, and longer periods of tonic immobility (Zulkifli et al., 1998). The timing of light cycles thus is a factor that may be a source of stress for animals maintained in captivity.

Light intensity also varies in different captive housing situations. Keeping animals in constant low light is a common practice aimed at reducing aggression, but it may in and of itself be detrimental to welfare (Martrenchar, 1999). On the other hand, bright light may also be stressful. Red deer kept under bright light conditions show more fearful behavior than did deer housed under dim light (Pollard and Littlejohn, 1994), and injuries due to fighting increase under bright light for turkeys (Moinard et al., 2001). These data suggest that light of high intensity may arouse some species in a way that is detrimental to their optimal maintenance in captivity.

Species also differ in their thresholds for light detection (for example, both dogs (Miller and Murphy, 1995) and cats (Gunter, 1995) are more sensitive to light stimuli than are humans), which may influence how they respond to light of varying intensity. When given a choice, species show differences in their preferences for lighting of different intensities, as indicated by the amount of time spent in each condition. Turkey poults, for example, appear to prefer lighting that is dimmer than what is preferred by ducklings (Barber et al., 2004). Rats also prefer lower light intensities, and the strength of this preference is dependent on eye pigmentation (with albino strains showing a stronger preference for dim light conditions (Blom et al., 1995; Schlingmann et al., 1994). Such strain differences may not be surprising, since increased rates of light-induced lesions to the eye are more common in albino rats, and also more common among rats housed in cages that are higher on a rack (and thus have a greater exposure to light) (Rao, 2001; Greenman et al., 1982).

Cage height is an infrequently addressed variable in many studies of captive animal behavior (Reinhardt and Reinhardt, 2000), but one that nonetheless may have a significant effect on animal welfare—at least in part due to differences in the amount of light received by animals housed in different tiers. While being housed at different heights subjects animals to many potential stressors (including different degrees of proximity to direct gaze by human caretakers), it also clearly subjects animals to differing amounts of ambient light (Shapiro et al., 2000). Such variability in perceived illumination may adversely affect animal welfare. For instance, long-tailed macaques housed in lower-tier cages (where less light is received) exhibit more abnormal behavior and less overall activity than do macaques housed in upper-tier cages (Shapiro et al., 2000). Similar effects of low light intensities have been found in rhesus macaques (Draper, 1965; Issac and De Vito, 1958).

Cage height affects the development and form of stereotypies in wild-caught roof rats housed in captivity (Callard et al., 2000), presumably because of the different light levels to which rats are exposed at different cage heights. In mice, being housed in cages higher in a rack system is associated with greater emotionality (a possible indicator of stress) and a greater likelihood of developing diabetes (Ader et al., 1991), a disorder that is promoted by stress (Carter et al., 1987). Similarly, laying hens housed in the top tier of a three-tier battery cage system show longer periods of tonic immobility and greater overall fearfulness of a number of different stimuli (Jones, 1985, 1987). Data such as these have resulted in recommendations for uniform

illumination in captive environments (International Primatological Society, 1989; National Research Council, 1996; USDA, 1991). Clearly, many researchers believe that availability of light can have a significant impact on captive animal well-being.

Wavelength is another attribute of light that may affect animal well-being. Animals differ from one another and from humans in their sensitivities to different light wavelengths, and this may affect their stress levels in captivity. Many species of birds, invertebrates, and some reptiles and mammals detect ultraviolet (UV) wavelengths of light, and may in fact require information provided by such wavelengths to inform decisions about foraging or social interactions (including mate choice). For these species, wavelengths of light in the short end of the electromagnetic spectrum are part of their color space, and therefore necessary for optimal perception of their surroundings (Cuthill et al., 2000).

In a few studies, deprivation of critical light wavelengths affects physiological measures in ways typically indicative of stress. Lab-housed rhesus macaques showed more abnormal behavior when maintained under an artificial lighting regime compared to natural full-spectrum light (O'Neill, 1989). Domestic chicks reared under UV-deficient light conditions show increased plasma corticosterone, along with reduced exploratory behavior (Maddocks et al., 2001). European starlings also show elevated levels of plasma corticosterone when housed in UV-deficient light conditions (Maddocks et al., 2002b). This species also shows a preference for UV light conditions when viewing potential mates, as do blue tits (Maddocks et al., 2002a,b). In budgerigars too, mate choice is affected by UV light (Pern et al., 2003). For some species, then, successful reproduction and maintenance in captivity may depend greatly on the availability of appropriate wavelengths of light.

While fluorescent lights can be used to increase available spectra for animals, these lights are accompanied by yet another potential problem for nonhuman animals. Although the illumination provided by fluorescent bulbs appears constant to humans, these bulbs emit light discontinuously. Their flickering is invisible to most humans under normal conditions, but might be detectable by a variety of species (D'Eath, 1998). For humans, the lowest flicker frequency at which images fuse so that no flicker is detected (referred to as the critical flicker fusion frequency, or CFF) occurs from about 45 to 60 Hz, depending on what part of the visual field is focused on the flickering image (Brundrett, 1974). However, for many animals, CFF is higher (D'Eath, 1998). Flicker fusion in dogs occurs at frequencies in excess of 80 Hz (Coile et al., 1989), and domestic chickens may have a CFF of about 105 Hz (Nuboer et al., 1992). At least some animals show a preference for higher-frequency fluorescent lighting (Greenwood et al., 2003), while others appear to prefer lower-frequency lighting (Widowski et al., 1992). Such discrimination suggests that animals can indeed detect some kind of difference between these two types of lighting— most likely, because of differences in their CFF. Yet we know very little about CFF in different species. Adding to the difficulty is the fact that CFF changes with where in the eye the flickering image is resolved, with age (Eisner and Samples, 1991), and in some species, with temperature (Schäfer et al., 1978). It is clear that much more needs to be learned about the visual worlds of captive species, and how light intensity, wavelength, and quality affect their behavior and physiology. Such information is essential to optimize well-being in captivity.

2.3. Odors

Virtually all mammals other than primates are considered macroosmatic—that is, they depend largely on olfactory cues (Slotnick et al., 2005). Although many macroosmatic species have evolved other sensory systems that are regularly used to direct their activities, their primary sense

nonetheless remains olfaction. In some cases, odors have been used as a form of environmental enrichment, with the goal of reducing behavioral indicators of stress (e.g., Jones et al., 2002; Pearson, 2002; Wells and Egli, 2004). However, for many animals living in captivity, the odors to which they may be exposed can be chronic sources of distress.

Prey animals in captivity, for instance, may be constantly exposed to the smell of their historical predators. There are abundant data to suggest that this is a source of stress. Studies of laboratory rats have shown that exposure to cat odor is sufficient to raise plasma levels of corticosterone (File et al., 1995) and increased blood pressure (Dielenberg et al., 2001), as well as to produce long-lasting changes in anxiety-like behavior (Adamec and Shallow, 1993; Perrot-Sinal and Petersen, 1997) and increases in defensive behavior (Adamec et al., 1998; Dielenberg et al., 2001). In fact, exposure to predator odor is so effective at eliciting arousal in rats that it is routinely used to induce a stress response in this species. Similar changes in behavior and/or physiology have been seen following exposure to predator odor in other species, such as voles (Perrot-Sinal et al., 1999), spotted frogs (Lefcort et al., 1999), crayfish (Hazlett and Schoolmaster, 1999), beaver (Engelhart and Mullerschwarze, 1995), fish (Jachner, 1995), hedgehogs (Ward et al., 1996), cotton-top tamarins (Buchanan-Smith et al., 1993), and wapati (Chabot et al., 1996).

The odor of conspecifics may also be stressful under some conditions. Frog species, for instance, actively avoid substrates that have been scent-marked by unfamiliar conspecifics, while showing a preference for substrates marked by themselves or by near neighbors (Waldman and Bishop, 2004). Among callitrichids, the scent marks of stressed individuals are investigated by conspecifics more frequently than those of nonstressed conspecifics (Epple, 1985), suggesting that animals can become aroused by detecting arousal in others. Chemical cues from conspecifics have been shown to affect the attractiveness of foods in rats (Galef, 2002), and odor cues from frustrated or frightened conspecifics inhibit rat behavior (Schultz and Tapp, 1973). A similar effect has been shown in pigs, which will avoid food hoppers sprayed with urine from a frustrated conspecific (Vieuille-Thomas and Signoret, 1992). These data suggest that a variety of animals may be able to detect distress in conspecifics based on odor cues alone, and that these odor cues themselves may be stressful to individuals perceiving them.

For many species, chemical communication is essential for normal social interaction and reproductive behavior. The influence of conspecific odor on development and maintenance of rodent sexual behavior is well-documented (Slotnick et al., 2005), but similar activating or inhibiting effects of conspecific odor on sexual behavior have been found for goats and sheep (Gelez and Fabry-Nys, 2004), marmosets (Barrett et al., 1990), giant pandas (Swaisgood et al., 2000), cattle (Cupp et al., 1993), and pigs (Dorries et al., 1995). To the extent that we wish animals maintained in captivity to be reproductively successful, it appears that we must attend to the effects of captivity on availability and potency of chemical cues.

One element of captivity that may interfere with these cues is routine cage cleaning. Many animals use scent marks to delineate territory or to indicate reproductive status, and for these species, the constant removal of these scent cues may be stressful. In response to cleaning, such species usually attempt to re-anoint their surroundings (Hediger, 1964). Because some species also increase rates of scent-marking when distressed (e.g., callitrichids; Epple, 1985), the effect of cage cleaning on rates of scent marking may be misinterpreted as indicative of stress. Nonetheless, it is clear that cage cleaning and subsequent removal of olfactory cues may indeed be stressful. Removing scent marks has been shown to increase aggression among group-housed mice, as does the transfer of bedding from a novel cage of conspecifics (van Loo et al., 2000).

Cage cleaning also results in increased tongue-flicking and investigatory behavior in captive rattlesnakes and stimulates efforts to remark cages in other snakes through a decreased latency to

defecate (Chiszar et al., 1980). Green iguanas in captivity similarly show a decreased latency to defecate in a clean cage (Morgan, personal observation), as do rats (Saibaba et al., 1996). Some species also show changes in behavior in response to odors that typically accompany many cleaning products. Pocket gophers, for instance, have been shown to actively avoid pine needle scent (Epple et al., 1996), and pungent smells (such as citronella) increase vigilance behaviors in mice (Kemble and Bolwahnn, 1997). In contrast, domestic cats show an attraction to bleach residue on the hands of handlers (Tromborg, personal observation). Other pungent odors associated with particular bedding types such as cedar or pine is associated with adverse impacts on the rodent liver (Davey et al., 2003) and immune system (Sanford et al., 2002). Taken together, these data suggest that an understanding of the impact that odor has on animals in captivity is essential for creation of captive environments conducive to animal well-being and reproduction (Kleiman, 1994).

2.4. Thermal and tactile experience

In the wild, many animals have the ability to migrate when ambient temperatures deviate from their preferred ranges. In captivity, however, the ability of animals to move when temperatures are other than optimal is greatly curtailed or absent altogether. In captivity, animals are routinely exposed to temperatures for which their species is not adapted. Species that evolved in warmer climates (such as elephants, lions, and giraffe) are housed in temperate zone zoos that see significant cold at different times of year, while species from colder climates (such as polar bear and penguins) are housed in zoos where snow rarely falls.

The consequences for animals under these conditions are very real, and often far from ideal. One of the authors worked at a national primate research center in the United States during graduate training, and remembers the number of frost-bitten tails each year that developed among rhesus macaques raised in field cages at that facility. Although the animals were provided with shelters and heat lamps during cold weather, frostbite nevertheless occurred, especially among subordinate individuals who were unable to command warmer and preferred resting perches. Temperature also affects the behavior of animals in ways that may not only reflect distress, but that may compromise the mission of the facility housing them. For instance, visibility to visitors of zoo-housed gorillas on exhibit has been shown to correlate negatively with increases in ambient temperature (Stoinski et al., 2002).

Extreme temperatures are well-known stressors, and indeed are often used as provocateurs in studies of behavioral and physiological responses to stress. Thus it should not be surprising to find temperature as a frequent source of discomfort and distress among captive animals. Domestic pigs, for example, show increases in salivary corticosterone when temperatures exceed 17 °C, while low temperatures increase huddling behavior (Hillman et al., 2004a) and high-frequency vocalization (Hillmann et al., 2004b) in this species. Distress calls in chicks increase with increases in temperature (Herbert and Sluckin, 1969), while infant rats separated from their littermates and dams emit more ultrasonic vocalizations at lower temperatures (Shair et al., 2003). Low temperatures (9 °C) result in a higher frequency of stereotypic behavior in Asian elephants (Rees, 2004). And rabbits show abnormal maternal and sexual behavior when temperatures get too high (Marai and Rashwan, 2004). Results from these studies and many others suggest that ideal thermal ranges are unique for each species and developmental age, making temperature control a particular challenge for captive animal management. To make matters more complicated, the effect that temperatures have on stress responses in animals appears to be dependent to some degree on individual differences, such as weight. Bigger pigs, for example, can tolerate larger ranges of temperatures compared to smaller pigs (Hillman et al., 2004a).

Social housing may also affect ideal temperature range. Group-housed mice, for instance, show temperature preferences that are a degree or so cooler in comparison with singly housed animals (Gordon et al., 1998).

In captive environments, aberrant social behavior is a common problem, and temperature can have a direct affect on such behavior—for good and for ill. Captive cichlids, for example, fight more at higher temperatures (Ratnasabapathi et al., 1992), while captive mice fight more at intermediate temperatures (Greenberg, 1972). Pigs play less at lower temperatures (Olsen et al., 2002), and huddle more (Hillman et al., 2004a), as do geckos (Shah et al., 2003). Captive infant baboons spend more time huddling with their mothers at lower temperatures, and spend more time away from their mothers at higher temperatures (Brent et al., 2003). Warmer temperatures increase "buller behavior" behavior in domestic cattle (in which steer repeatedly mount and ride a penmate until that penmate is injured or killed) (Blackshaw et al., 1997). And gerbils groom at different frequencies dependent on temperature (Thiessen et al., 1977). Some of these changes in behavior as a function of temperature have clear and direct impacts on animal well-being in captivity (e.g., "buller" behavior); others are a bit more subtle. To the degree, however, that we wish to maintain species-typical social behaviors in captivity, temperature may be one of many abiotic factors to consider.

Indeed, most animal welfare legislation explicitly dictates allowable temperature ranges for different species (Besch, 1990). Regulations such as these would suggest that maintaining optimal temperatures for animals is little more than a matter of adjusting thermostats in animal enclosures. However, in many cases the thermostats that control the onset or offset of heating or cooling units are not located in such a way as to accurately reflect the microclimate in the immediate vicinity of the animals (van Wagenberg et al., 2005). The placement of monitoring devices for temperature must be carefully considered, if we wish to ensure that temperature is not an unintended stressor in captivity.

2.5. Substrate

One way that animals can behaviorally thermoregulate in nature is by seeking microclimates with low surface temperatures (i.e., low longwave radiation). Alternatively, they may avoid sunlight or heat-releasing visible light (such as that produced by incandescent lighting)—so-called shortwave radiation (Langman et al., 1996). Most captive environments limit an animal's ability to thermoregulate in this way. Even if shade or shelter is provided to reduce direct exposure to heat or cold, the surfaces on which captive animals are maintained may prevent effective thermoregulation. In fact, many of the behavioral changes observed in animals in response to temperature (reviewed above) can be altered by changes in substrate.

Substrates that are common in captivity, such as concrete, gunite, tile, soil, grass, wood, rock, plastic, rubber, and/or metal vary in their thermal inertia—the speed with which they gain and lose heat. In addition to composition, the color of flooring or cage surfaces can also affect their thermal properties; darker colors tend to absorb heat, while lighter colors reflect it. To the degree that a given exhibit or captive environment is surrounded by surfaces with high thermal inertia and high heat reflectance properties, temperatures may exceed those preferred by an animal even when it has sought shelter in a shaded area.

Few if any studies, however, have been conducted to assess the thermal properties of common flooring materials employed in captive animal housing. In one study of thermal inertia in substrates commonly found in urban settings, concrete and wet soil were found to have the greatest thermal inertia; the substrate with the lowest thermal inertia was turf (Swaid, 1991).

Another study examined the thermal properties of light and dark-colored gunite surfaces in a zoo exhibit for pinnipeds. Light-colored gunite in this study reflected 41% of direct sunlight and effectively eliminated the cooling effect of any shaded areas in the exhibit; temperatures in shaded areas were as high at those in unshaded areas, resulting in a mean surface temperature of 33 °C (Langman et al., 1996). Painting the gunite a darker color, however, reduced its shortwave reflectance by 33%.

For animals that reside near ground level, ambient temperature is not merely a function of downward-directed infrared radiation from the sun and upper atmosphere, but also of the upward infrared radiation emitted by ground surfaces. When the temperature of the substrate exceeds that of the overlying air (as in the case of substrates with high thermal inertia such as concrete, stone, or gunite), temperatures immediately above the substrate can be much higher than ambient air temperatures would predict (Asaeda et al., 1996). Such observations suggest that the microclimate inside gunite-coated or similar exhibits may be very different from what we ourselves experience outside of the exhibit.

Variations in local microclimate or in the thermal properties of substrates do contribute to differences in behavior and well-being. Mice with inadequate bedding for burrowing, for instance, show an increased metabolic rate and reduced core body temperature (Gordon, 2004). Cooling of the floor when temperatures exceed 25 °C reduces lying behavior in pigs, and increases feeding and growth rate (Huynh et al., 2004). Animals also vary in their preferred substrate temperature. Farrowing sows prefer warmer substrates than they do at other times in their life cycle (Phillips et al., 2000), suggesting that pigs seek environments conducive to maintaining neonatal piglet body temperature. As temperatures rise, juvenile pigs prefer to rest on cool bare concrete, but at lower temperatures, warmer straw-bedding is preferred (Fraser, 1985). Cattle prefer straw bedding to rubber mats when temperatures are low (Manninen et al., 2002). And unsheared sheep prefer cooler substrates for resting, while sheared sheep prefer resting surfaces with lower thermal conductivity (Faerevik et al., 2005).

But temperature is not the only quality of substrate in captivity that may impact an animal's well-being. Different surface materials also vary in their hardness and resistance to compression, and thus in the stress that they put on legs and joints (Bargai and Cohen, 1992). Surface materials also vary in how much friction they offer, and thus how much resistance to slipping they provide (van der Tol et al., 2005; Applegate et al., 1988). Such factors are critical contributors to lameness, and as such, play a major role in captive animal well-being (Grandin and Johnson, 2005). Additionally, smooth surfaces (although easier to clean) are also more acoustically reflective (Forthman, 1998; Tromborg, 1993); given the impact that sound may have on animals in captivity (reviewed above), this aspect of housing substrate is another potential stressor.

When animals are given a choice, they appear to select substrates that vary not only by their thermal qualities, but by their softness and/or the footing purchase they provide. Cattle appear to prefer substrates that afford better footing and therefore less chance of slipping (Hultgren, 2001). Mice prefer running wheels made of material that offers a better purchase when running (Banjanin and Mrosovsky, 2000), and bedding material that is soft enough to allow for burrowing and nest construction (Ago et al., 2002). Sheared sheep prefer straw substrates to bare wood or rubber mats, and spend less time recumbent when provided with straw immediately after shearing (Faerevik et al., 2005). Young pigs prefer substrates that are most similar to soil, and spend the least time on concrete when given a choice (Beattie et al., 1998). Hamsters prefer solid flooring with bedding over wire mesh flooring, and spend their time differently when housed on wire mesh compared to solid flooring (Arnold and Estep, 1994). Rats prefer large

particle bedding (such as wood shavings or paper bedding) over wire mesh or small particle bedding (e.g., sawdust) (van de Weerd et al., 1996), and solid flooring over grid or wire mesh flooring, if given a choice (Manser et al., 1995). The nature of the substrate also appears to affect commonly accepted physiological measures of stress. For instance, grid and plastic floors appear to be stressful for rats, as measured by significant changes in blood pressure, heart rate, and body temperature compared to when the animals are housed in wood chip bedding (Krohn et al., 2003). Rats housed on coarse sawdust show greater sensitivity to pain than do rats housed on finer sawdust (Robinson et al., 2004), and rats housed in cages with wire mesh floors rapidly develop nerve injury and soreness in the hindlimbs (Mizisin et al., 1998). Housing substrate can even influence cognitive ability—homing pigeons housed in plastic containers (even when provided with adequate ventilation) show impaired navigational abilities compared to pigeons housed in other kinds of containers (Sandberg et al., 1999). The impact of housing substrate on cognition in this case appears to be a consequence of stress induced by the nature of the container. Taken together, these observations suggest that the nature of the substrate may have a substantial influence on animal stress in captivity.

Many species of animal build nests, both for the raising of young as well as for resting and shelter. In a smooth-floored or barren captive environment, nest building is not possible, and the inability to do so may result in aberrant behavior that suggests distress. Animals will work for access to nest-building material (Anna et al., 2002; Cooper and Appleby, 2003), suggesting that nest-building is a behavioral need in some species.

In addition to allowing for species-typical nest building behavior (when appropriate), complex substrate in the form of earth, straw, or other similar bedding also provides manipulanda, which can reduce boredom and the frequency of associated abnormal behaviors, and increase the frequency of species-typical behaviors (Baker, 1997; Chamove et al., 1982; Fraser et al., 1991). In some cases, a more complex substrate can also improve social interactions, perhaps by providing retreat opportunities for subordinate animals (Armstrong et al., 1998), or by providing an alternative outlet for exploratory behavior. Pigs housed in barren pens, for example, direct more chewing and rooting behaviors at penmates than do pigs raised in pens with deep straw bedding (de Jong et al., 1998). Ultimately, providing captive animals with a more complex substrate can enhance the range of behavioral opportunities and conceivably, reduce stress.

The data we have reviewed thus far suggest that a variety of sensory elements in the environments of captive animals – including the quantity, quality, and periodicity of light, the presence or absence of particular odors, the pitch, frequency, and sound pressure level of sounds, and the heat indices, slickness, softness, and manipulability of substrate – have potential as sources of chronic stress. Unfortunately, many of the components of these sensory elements that are most disturbing to captive nonhuman animals are not readily detectable by human caretakers. Furthermore, our knowledge of the sensory worlds or umwelts of most species is extremely limited, and thus our ability to predict what kinds of stimuli might be stressful to a given animal is impaired. In order to optimize animal well-being in captivity, it is imperative that we have a better understanding of species-typical sensory abilities and their role in natural histories. Much work remains to be done in this arena.

Nonetheless, it is our charge as animal stewards interested in conserving natural behavior in captivity to promote animal well-being by reducing sensory sources of stress whenever we are able to do so. To do this with our limited human sensory capabilities requires technological assistance. Table 1 lists the potential sensory stressors we have identified, and some of the

Table 1
Potential environmental stressors and means by which to measure them

Potential source of stress	How to measure	Suppliers	Additional information (if available)	Species particularly at risk
High sound pressure level	Commercially available dB meters	D.A.S. Distributiion (www.dasdistribution.com) Radio Shack (www.radioshack.com) Action Electronics (www.action-electronics.com) Scantek Inc. (www.scantekinc.com) Pulsecho Systems (www.pulsecho.com) Bruel and Kjaer (www.bkhome.com) IET Labs (www.ietlabs.com)		All
Ultrasonic sound[a]	Commercially available bat detectors	Bat Conservation International (www.batcatalog.com), BatBox LTD (www.batbox.com), Laar Techologies (www.laartech.biz)	Comparing bat detectors (www.birds.cornell.edu/ MacaulayLibrary/ contribute/equipBat.html)	Rodents; species that hunt rodents; marine mammals; chiropterans
Infrasonic sound[a]	Geophones Low-frequency sensitive microphones Low-frequency sensitive preamplifiers	Geo Space, L.P. (www.geospacelp.com) Earthworks (www.earthworksaudio.com) Sound Devices (www.sounddevices.com)		Large species (e.g., elephants, giraffe, rhinoceros, large marine mammals, okapi, crocodilians, hippopotamus); species that live underground (e.g., mole rats)
Overall light levels	Commercially available light meters	Professional Equipment (www.professionalequipment.com) DAS Distribution (www.dasdistribution.com)		All
Light spectra	Commercially available light meters	Professional Equipment (www.professionalequipment.com) Spectrum Technologies (www.specmeters.com)		
Presence or absence of UV light	Commercially available light meters			
Flicker in fluorescent lights	Typically measured indirectly using commercially available voltage meters			Species with high photoreceptor densities in the eye or high densities of one-to-one wiring between photoreceptors and ganglion cells in the eye; insects

[a] For sound pressure level of infrasonic and ultrasonic sounds, sounds must be recorded, slowed down, and played through a dB meter. Infrasound and ultrasound can also be assessed using using sound spectra analysis hardware and software.

technologies available to measure them. It is our hope that this list will help animal caretakers to better assess the sensory stress potential of captive environments.

3. Confinement-specific stressors

Environmental stimuli such as those reviewed above are by definition everywhere; the primary difference between such stimuli in nature and the same stimuli in captivity is in the animal's ability to control its exposure to these stimuli. In the wild, an animal can generally move away from aversive light or sound; it can seek shelter from undesirable climactic conditions, dig into the earth to cool itself, and time its daily activities to coincide with whatever environmental variables are most suitable. The captive animal, however, has no such luxury. In general, animals in captivity have little or no control over the timing, duration, and/or nature of the light, sound, odors, or temperatures to which they are exposed. For the most part, this lack of control is a direct result of confinement.

In addition to reducing or eliminating control over exposure to a number of environmental variables, confinement in captivity brings with it a host of other potential stressors, largely in the form of restricted choice. Whether in zoos, laboratories, or agricultural settings, animals in captivity are limited in their freedom of movement, their ability to retreat from conspecifics and from human caretakers, and the timing and nature of their food and mate choices. Below, we review data suggesting that each of these factors may be potential stressors for captive animals.

3.1. Restricted movement

It seems a matter of common sense that one of the greatest potential stressors in captivity would be restriction of movement due to small cage or pen size. Yet this is an area in which intuitively obvious answers may lead one astray in any efforts to improve conditions for captive animals. Current cage size standards in the United States and elsewhere are based primarily on arbitrary professional judgment, and not empirical analyses. And the empirical studies that do exist have produced mixed results.

Hediger (1955, 1964) considered restricted movement due to space limitations to be one of the primary contributors to captivity-induced stress, and some of the earliest studies of abnormal behavior in captive animals supported this contention (e.g., Levy, 1944). More recent work has also suggested an adverse effect of confinement in small spaces. In one study of the impact of captivity on 35 different species of carnivore, infant mortality in captivity and stereotypic locomotion in the form of pacing was found to correlate positively with species home range size in the wild (Clubb and Mason, 2003, 2007), suggesting that the impact of enclosure size on captive animals is a matter of natural history to some degree. In other studies of group-housed pigs, housing the animals in smaller pens increased rates of agonistic behavior (Lammers and Schouten, 1985; Wiegand et al., 1994). A similar increase in aggression with decreased enclosure size has been observed in buffalo calves (Napolitano et al., 2004), male turkeys (Buchwalder and Huber-Eicher, 2004), and captive dama gazelle (Cassinello and Pieters, 2000).

Overall activity and conversion of feed to body weight are two other variables that appear to be compromised for some species when housed in smaller enclosures. Pigs in smaller pens, for example, spend more time sitting or standing motionless, and show reduced growth rates compared to pigs housed in larger enclosures (Pearce and Patterson, 1993). The same effect of pen size on growth rate has been shown in sheep (Horton et al., 1991). These effects of pen size on growth rate have been interpreted by authors as indicators of chronic stress (recall that suppressed

growth is a common physiological consequence of chronic stress). Impaired growth rate due to stress is clearly undesirable in animals such as pigs that are raised for agricultural purposes. However, such impairment is also undesirable for those interested in conservation of endangered species in captivity; captive populations will fail to thrive if restricted space and subsequent stress increase rates of aggression and/or delay development through slowed growth rates.

Adverse impacts of enclosure size have also been found on rodent behavior, particularly with respect to sex and reproduction. Rats housed in smaller cages, for instance, show less frequent mounting, reduced intromission, reduced ejaculation frequency, and longer post-ejaculatory intervals compared to rats housed in larger pens (Saito et al., 1996). To the extent that crowding and spatial restriction suppresses reproduction in other species, it is a serious problem for those interested in sustaining captive populations.

Other studies of the effects of cage size on well-being have been less equivocal. Increasing enclosure size for great apes species, for instance, has been found to have little or no effect on behavior in one study (Wilson, 1982), while in another specifically of zoo-housed orangutans, enclosure volume and usable surface area predicted behavior activity levels (Perkins, 1992). Some authors have found a decrease in rates of abnormal behavior concomitant with an increase in cage size (e.g., Draper and Bernstein, 1963; Paulk et al., 1977). But in other studies, more ambiguous results have been found. Transferring a young gorilla to a larger, more naturalistic exhibit, for instance, decreased play behavior, and increased some stereotypies while reducing others (Goerke et al., 1987). Similarly, moving an adult chimpanzee from a small cage to a larger, more open naturalistic exhibit reduced abnormal behavior, but also activity in general (Morgan et al., 2002). Housing singly caged rhesus monkeys in larger cages did not reduce abnormal behavior (Line et al., 1990), even when the new cage was six times larger than their standard cage (Kaufman et al., 2004). The same lack of effect of a larger cage on abnormal behavior has been observed in captive cynomolgus monkeys (Crockett et al., 1995). And in one study, the frequency of abnormal behavior actually increased with an increase in cage size (Bayne and McCully, 1989)!

Increasing cage size may actually be stressful for prey animals that are hunted in open spaces, such as small rodents (Hughes, 1969). And even for species that in the wild live in what appears to our human eyes to be substantial open space do not always prefer the largest available living spaces. Dolphins given a choice between three pool sizes choose to spend most of their time in moderate-sized areas, rather than the largest area available (Shyan et al., 2002). Findings such as these have led some authors to suggest that species natural history is a better predictor of animals' responses to confinement and enclosure size than is any other variable (Clubb and Mason, 2003; Shyan et al., 2002). Unfortunately for many species in captivity – particularly domestic species – data on natural habitat use are limited or nonexistent. Nonetheless, it may well be that it is not the quantity of space available to the animal which is important, but its quality—what it affords animals in the way of behavioral opportunity.

3.2. Absence of retreat space

One of the behavioral opportunities that is limited for animals in captivity is their ability to move away from one another or from human passers-by. The lack of sufficient retreat space is a significant potential stressor for captive animals. Whether on exhibit at zoos and aquaria, housed in compartment-style caging in labs, or in intensive management systems in agricultural settings, animals in captivity are often maintained under conditions that afford little or no concealment opportunity. For many species, this is clearly stressful.

Bank voles raised in barren and open caging, for instance, show more stereotypies than do voles raised in caging with sufficient bedding to serve as a burrow (Cooper et al., 1996). Gerbils in barren caging develop more stereotypic digging than those reared in cages with artificial burrows (Waiblinger and König, 2004; Wiedenmayer, 1997). Mice show more stereotypic wire-gnawing when housed in barren cages compared to when provisioned with cardboard tubes in which to hide (Wurbel et al., 1998). Rabbits raised in conventional barren caging show more restlessness, bar-gnawing, timidity, and self-grooming than do rabbits raised in caging enriched with a shelter and nesting material (Hansen and Berthelsen, 2000). Rats in barren cages without burrows show greater fearfulness and less exploratory behavior than do rats housed in cages furnished with hiding places (Townsend, 1997). Free-range broiler chickens range less when tree cover is reduced or absent (Dawkins et al., 2003), and domestic hens rest and preen less with less cover (Newberry and Shackleton, 1997). Pygmy goats and Romanov sheep in a petting zoo showed higher rates of undesirable behavior (threats or aggression directed at visitors) when they were unable to retreat (Anderson et al., 2002). Captive anoles show longer and more persistent bouts of tonic immobility when housed in cages that provide no hiding areas (Henning and Dunlap, 1978). And mice in barren cages self-administer anxiolytic drugs more often than do mice in cages enriched with hiding places (Sherwin and Olsson, 2004). These data suggest that a wide variety of species from varying taxa require some opportunity for concealment for their optimal well-being.

Adding retreat spaces improves many indicators of animal welfare. Mixing unfamiliar animals is a sometimes unavoidable part of captive husbandry, yet in many species, such mixing triggers aggressive behavior. Provision with retreat space, however, can reduce aggression in some circumstances in which unfamiliar or incompatible animals must be housed together Young pigs in newly formed groups, for instance, fight less when hiding places are available (McGlone and Curtis, 1985). Provision of a nest box increased fighting and plasma corticosterone in mice, but also improved immune system function and increased the frequency of positive social behaviors (Marashi et al., 2003). And provision of a camouflage barrier reduced aggression and stereotypic behavior in zoo-housed gorillas (Blaney and Walls, 2004). These data suggest that when animals are housed in social situations that are potentially stressful, the presence or absence of adequate retreat space influences how those situations affect their well-being.

In many cases, data suggest that the reduction of distress provided by the addition of retreat space is directly related to the need to cope with potential threat. Animals show a preference, for example, for retreat space that is easily defended. Thick-tailed geckos prefer hiding places that are narrow and difficult to enter (Shah et al., 2004). And mice prefer nest boxes with only one opening, resting in them with their heads oriented towards the opening (van de Weerd et al., 1998). Animals also appear to prefer retreats that prevent detection by predators; when given a choice, rats prefer opaque enclosed shelters, as opposed to transparent shelters (Manser et al., 1998; Patterson-Kane, 2003). These data support the contention that a reduction or absence of retreat opportunities and hiding places can be a source of distress for animals in captivity. Once again, it may not be quantity of space but what complexity of space affords an animal that determines enclosure impacts on well-being.

3.3. Forced proximity to humans

In many instances, the perceived threat from which animals seek to escape through the use of a retreat space are ourselves—the human caretakers of these animals. Particularly for animals housed in zoos, proximity to humans may be greater than is comfortable for some species. Many zoos struggle with the conflict that often exists between what might be best for an animal's well-

being, and the need to provide paying visitors with what they paid for—the opportunity to see exotic animals. Some zoos known to the authors meet visitor pressure for viewing the animals by employing forced lockout, in which animals are barred from re-entering their off-exhibit holding areas during the times that the zoo is open to the public. In others, visitors are allowed close contact in a variety of ways (i.e., through petting zoos, live animal presentations, bringing animals out into the zoo grounds while visitors are present, or allowing some species to range freely throughout large enclosed exhibits or throughout the zoo) (personal observation; Hosey, 2005). To be fair to zoos, the underlying intention for increased visitor-animal interaction is to promote the empathy and sense of connectedness needed to improve attitudes and behavior with respect to conservation. Regardless of intention, however, forced proximity to or contact with humans can be deleterious to animal well-being.

Species vary in their flight distances from humans (reviewed in Tarlow and Blumstein, 2007), but the ability of zoo exhibit designers to take this information into account when a new exhibit is constructed may be limited. In some cases, the total space available for a new exhibit may limit the amount or quality of retreat space that can be allocated to a species. In other cases, the data available on species flight distances are sparse or variable. In the case of zoos in which age of the facility, finances, or imperfect knowledge of species needs result in exhibits with limited retreat space for their residents, visitor impact on many zoo animals may be enormous. On a day-to-day basis, visitors to a zoo may be one of the few unpredictable variables that animals experience; feeding times, cage cleaning, and animal caretakers may be relatively consistent, but the number of visitors and visitor behavior varies from moment to moment. To the degree that this variability breaks up an otherwise monotonous existence, it may be have a positive effect on well-being (Morris, 1964). However, visitors also vary in the degree to which they attempt to interact with captive animals, and in the nature of those attempted interactions. For many species, it is clear that these visitor behaviors affect *their* behavior and levels of arousal.

The visitor effect has been best documented in nonhuman primates (Hosey, 2005). Zoo-housed primates direct more behavior at active audiences, for example, and show greater overall activity when audiences are active (Chamove et al., 1988; Hosey and Druck, 1987; Mitchell et al., 1992b)—which of course attracts more visitors! For some species (e.g., golden-bellied mangabeys), visitor presence increases within-group aggression, and animals selectively direct aggression to different visitor targets (Mitchell et al., 1991, 1992a). Even in laboratory settings, human activity levels correlate positively with intraspecific aggression in primates (Lambeth et al., 1997).

In addition to promoting aggression, human presence appears to reduce the frequency of species-typical behaviors, and in some cases, overall activity. The presence of visitors, for example, decreases play and other positive social behavior in cotton-top tamarins (Glatston et al., 1984). In one study of zoo-housed chimpanzees, large crowds of visitors were associated with a decrease in observed foraging, grooming, and play (Wood, 1998). In another study of zoo-housed leopards, overall activity was suppressed when visitors were present, and large increases in visitor numbers resulted in increased pacing (Mallapur and Chellam, 2002), a behavioral indicator of agitation or stress. Similar effects of visitor numbers have been observed with visitor presence in captive grey-cheeked mangabeys (Hall et al., 2005) and Soemmerring's gazelle (Mansour et al., 2000). In one zoo, wild-caught capybara showed increased escape behavior whenever keepers entered the exhibit, despite having been in captivity for over 2 years (Nogueira et al., 2004). Similar retreat behavior has been shown in captive dolphins used in a ''swim-with-a-dolphin'' program (Kyngdon et al., 2003). And a study of the effects of human presence on 12 species of zoo-housed ungulate found that vigilance increased when keepers were outside of the exhibits, while feeding behavior decreased when keepers were inside the exhibits.

Vigilance behavior also differed by sex, with females tending to show greater vigilance (Thompson, 1989). (Recall that increased vigilance and overall arousal are putative behavioral indicators of stress in many species—including our own.)

Physiological indicators also suggest that at least in some cases, human proximity is stressful for captive animals. Urinary cortisol is positively correlated with visitor numbers in zoo-housed spider monkeys (Davis et al., 2005), and the presence of human caretakers engaged in routine husbandry tasks increases heart rate in lab-housed rhesus macaques (Line et al., 1991). Heart rate in lab-housed rhesus macaques continues to increase in the presence of a human observer, even after 2 years of study during which time all behavioral responses to observation seemed to have ceased (Line, Morgan, and Markowitz, unpublished data). The presence of a human also results in stress-induced hyperthermia in farmed silver foxes (Bakkan et al., 1999). And in one review of black rhinoceros breeding success in U.S. zoos, animal mortality was positively correlated with the degree of public access to the animals (Carlstead et al., 1999).

In addition to forcing proximity to humans, however, the maintenance of animals in captivity typically demands their direct handling. Evaluating the effects of handling by humans on nonhuman animals can be challenging, since the word ''handling'' is used to refer to a wide variety of procedures, from lifting an animal out of its home cage, holding or restraining it, performing cage maintenance with the animal present, or moving the animal from one place to another. Nonetheless it is clear that direct handling is stressful to animals—indeed, it has been used as an operational definition of stress in many studies.

Animals living in captivity almost by definition are subject to at least occasional handling by humans, and in many cases, this has been shown to be stressful. In one study, for example, handling by humans adversely affected immune responses of laying hens (presumably because of stress), despite the fact that the intention of the handling was to reduce fear of humans (Barnett et al., 1994). And removal of wool by shearing (which involves intensive handling) increases heart rate and plasma cortisol in domestic sheep more so than does social isolation or loud sound (Hargreaves and Hutson, 1990).

At the same time, handling and/or close contact with humans has been advocated as a form of environmental enrichment, particularly for social species housed in isolation (such as primates (APHIS, 1999) or dogs (Wolfle, 1989)). In one study, increased positive human interaction with chimpanzees was associated with decreases in abnormal behavior, increased social grooming, and reduced aggression (Baker, 2004). But the effect of human contact – even on so-called ''social'' animals – varies wildly depending on the nature of that contact, and the individual animal's past experiences with humans (Hemsworth, 2003). Not surprisingly, aversive experiences with humans result in animals that are more fearful of humans and more distressed by human presence, and this is reflected both behaviorally and physiologically. For example, pig farms at which sows showed a greater fear of humans had a greater percentage of stillborn piglets (Hemsworth et al., 1999). Pigs that had been rebuffed by humans or inconsistently treated showed a longer latency to approach humans than did pigs that had more pleasant interactions with humans (Hemsworth et al., 1987). Dairy heifers that have unpleasant experiences with humans show a greater latency to approach humans and higher plasma corticosterone than do heifers that have pleasant interactions with humans (Breuer et al., 2003). And milk yield is lower on dairy farms where handler attitudes towards the animals are negative and behaviors of handlers directed towards the cattle are more aggressive (Waiblinger et al., 2002).

In comparison, positive interactions with humans can result in improved well-being. Stump-tailed macaques that have ''friendly'' relationships with their caretakers are less disturbed by routine husbandry and approach caretakers more often (Waitt et al., 2002). Gently handled

broiler chickens show less fear of humans and less plasma corticosterone than do nonhandled birds (Hemsworth et al., 1994). Similarly, beef calves allow touch by a human more rapidly if they have had extensive previous positive contact with humans (Boivin et al., 1997). And female pigs that received pleasant handling also had higher rates of pregnancy compared to pigs that received unpleasant handling (Hemsworth et al., 1986a). Part of what pleasant handling appears to involve is meeting the animal on its own terms. For instance, pigs approach a human more readily when the human does not approach them. They are also more willing to approach a human if the human squats down rather than stands, does not wear gloves, and does not initiate interaction or approach (Hemsworth et al., 1986c).

Animals also readily discriminate between individual humans. For instance, laboratory rats show active avoidance of unfamiliar handlers, and approach familiar humans (Davis et al., 1997). Beef cattle also avoid familiar humans less than unfamiliar humans (Boivin et al., 1997). In the authors' experiences at one national primate research center, different classes of personnel (such as maintenance crew, animal caretakers, and research scientists) each wore different-colored uniforms or lab coats, and animals clearly discriminated between humans with these different ''coat colors'' through their behavior, showing maximal agitation when confronted by humans in white lab coats (the ''uniform'' of generally invasive vets or research scientists). Data such as these suggest that human contact can be both a ''blessing'' and a ''curse'' to animals living in captivity, depending on the type of human interaction.

3.4. Routine husbandry

Perhaps part of the reason for captive animals' distress in the presence of humans is due to the association of aversive routine husbandry events with their human caretakers. Certainly there are specific types of routine events that are reliably signaled by the presence of specific humans or human tools. For instance, walking into a laboratory housing rhesus macaques while carrying leather gauntlet gloves used for handling animals for aversive procedures is so arousing to the animals that we have used it specifically to induce a stress response in our subjects!

Data documenting the effects of routine husbandry procedures on the well-being of captive animals are sparse, but those that do exist suggest that what we humans may think of as routine is anything but to our animal charges (Balcombe et al., 2004). Even repeated events such as cage-cleaning continue to evoke physiological and behavioral responses that are commonly associated with stress. For instance, heart rate in captive primates increases during daily feeding and cage cleaning (Malinow et al., 1974) and monthly cage changing (Line et al., 1989). Similar effects are seen in rats (Duke et al., 2001; Saibaba et al., 1996; Sharp et al., 2003a). Interestingly, heart rate also increases significantly in rats that are mere ''bystanders'' or witnesses to routine events such as cage-changing, vaginal lavage, or decapitation (Sharp et al., 2003b). It is likely that routine events such as cage cleaning, cage changing, veterinary examination, or implementation of typical experimental procedure adversely affect most animals in captivity.

3.5. Restricted feeding and foraging opportunities

Many animals in their natural habitats spend a large portion of their daily activity budget in the search for and consumption of food (Herbers, 1981). In captivity, however, food is generally provided. Often this food is substantially different from what the animals would consume in nature; it may be more condensed, higher in protein, different in texture, and lower in fiber than a typical ''wild'' diet, and generally takes much less time to eat. A typical ration at

one U.S. national primate research center for a single feeding of singly caged female rhesus macaques was five large monkey biscuits (Morgan, personal observation); surely a much more compact meal than macaques would normally consume in the wild. The hardness of the monkey biscuits, however, slowed consumption; often, the animals held the biscuits in their cheek pouches for half an hour or so to soften them before attempting to eat them.

Other than their hardness, such foods provided little in the way of a challenge for the macaques such as they might be faced with if they were foraging on their own. Monkey biscuits do not have to be found, harvested, or (other than softening) processed before consuming them. For animals living in captivity, feeding oneself generally requires minimal effort.

Many studies have shown that animals will perform work to obtain food (Coulton et al., 1997; Inglis and Ferguson, 1986; Inglis and Shepherd, 1994; Menzel, 1991; Reinhardt, 1994), even when the same food is freely available to them. This phenomenon has been called "contrafreeloading," and some data suggest that animals in barren environments are particularly likely to display it. For example, in one study of laboratory rats, animals reared in enriched environments showed little or no tendency to contrafreeload, while rats reared in impoverished environments showed a strong preference to work for food over obtaining the same food when it was freely available (Colburn and Tarte, 1976). Such data support the argument that foraging is an inherently rewarding appetitive act, and one for which animals may have a behavioral need. Appetitive behaviors are searching behaviors presumably motivated by an "appetite" for a particular stimulus (Wallace, 1979); in this case, the stimulus would be a potential food item. Some authors have speculated that the frustration of appetitive behavior results in locomotor stereotypies (Mason, 1993), as animals attempt to "search" for food in a restricted environment. Some data support this hypothesis. For example, in one comparative study of rates of stereotypies in eight species of captive primate, omnivorous species showed significantly more stereotypies than did frugivores or folivores; the authors interpret this difference as due to the greater food search and handling time for omnivores that is limited in captivity (Marriner and Drickamer, 1994). In another study, restricting the feeding of captive giraffe in zoos resulted in increased locomotor activity (perhaps due to food-seeking), compared to free-ranging giraffe (Veasey et al., 1996); over time, such increased activity could result in pacing. Restricted feeding also correlates positively with stereotypic licking in giraffe and okapi (Bashaw et al., 2001), and stereotyped chain-chewing in gilts (Appleby and Lawrence, 1987). Conversely, requiring animals to work for their food appears to improve behavioral indicators of well-being. For instance, providing part of the routine diet in an enrichment device (the "Equiball") that requires some work to extract the food results in reduced stereotypic behavior in stabled horses (Henderson and Waran, 2001). Similarly, a foraging device that requires group-housed rats to search for food results in reduced aggression (Johnson et al., 2004). Provisioning captive chimpanzees with straw bedding and scattered food increases the animals' foraging time, since part of their diet is now hidden in the cage substrate. Such enrichment also decreases the frequency of regurgitation and reingestion, and increases play and overall activity (Baker, 1997). Presenting lion-tailed macaques with intact vegetables that require more processing time increases their overall feeding time, food intake, and range of foods eaten compared to provisioning them with the same foods chopped into smaller pieces (Smith et al., 1989). Puzzle feeders reduce some (but not all) stereotypic behavior in captive rhesus macaques (Novak et al., 1998). Providing a walrus with a trough of rocks in which to forage reduces stereotyped swimming and increases species-typical foraging behavior (Kastelein and Wiepkema, 1989). And hiding food throughout the exhibit increases exploratory behavior and decreases inactive behavior in leopard cats (Shepherdson et al., 1993).

Data such as these support the argument that reduced opportunities for foraging in captivity may be inherently stressful.

Another aspect of feeding in captivity that is not found in nature is its predictability. Often, the exact nature of the diet is invariable; animals are offered the same foods day after day. Some data suggest that such invariability is undesirable to animals. For example, trainers of racehorses correlate abnormal behavior in their equine charges with restricted variety of diet (McGreevy et al., 1995). When horses were offered four versions of a concentrated diet that varied only in flavor and not in nutritional value, they nonetheless sampled from each of the flavors (Goodwin et al., 2005), suggesting a motivation for variety that the authors assert reflects the natural patch foraging behavior that horses show in the wild.

Invariability of the diet is not the only predictable aspect of feeding in captivity; most animals are also fed at specific and invariant times of day. The predictable availability of food in some cases appears to generate abnormal behavior. For instance, stereotyped pacing and other repetitive locomotor activity increases as feeding times approach and animals anticipate the arrival of food (Friend, 1999; Vickery and Mason, 2004; Vinke et al., 2002; Waitt and Buchanan-Smith, 2001). In one study of captive chimps, making feeding time unpredictable reduced abnormal behavior and overall inactivity (Bloomsmith and Lambeth, 1995). In contrast, reducing the reliability of signals announcing food arrival increased aggression in group-housed pigs (Carlstead, 1986). And in laboratory cats, unpredictable feeding times were correlated with higher levels of urinary cortisol (Carlstead et al., 1993b). In this latter study, however, a number of variables were manipulated to produce a ''stressful'' environment of which unpredictable feeding time was only one.

Finally, provisioning with commercially prepared, easy-to-eat diets allows little opportunity for captive animals to engage in species-typical food handling or processing. Particularly for carnivores, thwarted hunting prospects appear to be stressful. In comparison, providing some opportunity for species-typical hunting behavior has been beneficial for fishing cats (Shepherdson et al., 1993), polar bears (Markowitz, 1982), and cheetahs (Lindburg, 1998). Providing live fish in a pool reduced stereotypic behavior in captive tigers, and provisioning with horse leg bones did the same, both for lions and tigers (Bashaw et al., 2003). Note that in addition to providing animals with greater opportunities to engage in species-typical feeding behaviors, the techniques employed in these studies also increased the variety of available diet. It is therefore somewhat impossible to determine with any certainly which manipulation (increasing behavioral feeding opportunity or increasing dietary variability) was responsible for any observed effect.

Easy-to-eat diets have also been found to have deleterious effects on carnivore dentition (Haberstroh et al., 1984; Vosburgh et al., 1982; Wenker et al., 1999); feeding whole-prey items in contrast improves dental condition (Lindburg, 1998). In addition, one study of large cats in zoos showed that whole-carcass feeding reduced stereotypic behavior in off-exhibit areas, but increased hiding behavior on exhibit (McPhee, 2002). The net benefit from intact carcass feeding to carnivores in captivity has yet to be determined.

3.6. Abnormal social groups

Most of the animals employed in laboratories or in agriculture are social species, as sociality is one of the characteristics of a species that facilitates the process of domestication (Price, 1984). Yet despite this we often maintain these animals in total or near total isolation from conspecifics. For many animals in captivity, such isolation is clearly stressful. In fact, social isolation has been

used to induce stress in many research investigations. The data resulting from these and similar investigations show an adverse effect of such isolation.

Singly housed laboratory dogs, for instance, display more abnormal behaviors than do group-housed dogs (Hetts et al., 1992; Hubrecht et al., 1992). Isolated piglets displays more escape attempts and less play behavior than do group-housed piglets (Herskin and Jensen, 2000). Dairy calves raised in isolation are more fearful than are group-reared calves (Boe and Farevik, 2003). Separating ewes from conspecifics increases respiration rate, serum cortisol, vocalization, and locomotion—all of which can be reduced by the addition of a single conspecific pen partner (Carbajal and Orihuela, 2001). Similar effects of social isolation on physiological and behavioral parameters associated with stress are found in rats (Genaro et al., 2004; Weiss et al., 2004) and cattle (Boissy and Le Neindre, 1997). And the adverse impact of social isolation on primates is so profound that it has generated an entire body of literature in and of itself (perhaps best known through the work of Mason (e.g., Mason and Fitz-Gerald, 1962; Mason, 1991b) and Harlow (e.g., Harlow and Harlow, 1971). Adding to findings such as these is the fact that many animals will do work to gain access to conspecifics. Given a choice between working for food or access to a social companion, for instance, tufted capuchins will work for social contact over food—even after several hours of food deprivation (Dettmer and Fragaszy, 2000). Singly housed dairy calves (Holm et al., 2002) and rats (Patterson-Kane et al., 2002) will also work for access to a social companion. For some species, social isolation is without doubt a stressful experience.

In other captive situations, animals are maintained in social groupings that would not generally occur in nature (e.g., Stoinski et al., 2001). Japanese macaques, for example, live in multi-male, multi-female groups in the wild. Yet one of the authors works on occasion at a zoo in which an exhibit of this species consists entirely of juvenile males. These animals show a great deal of social tension and very little natural activity, engaging instead in intensive monitoring of the others in their group. In Boston, Massachusetts, the recent exploits of a young gorilla named ''Joe'' made national news as he repeatedly escaped from his outdoor exhibit and on one occasion, even left the zoo grounds before he was recaptured. Joe was the only sub-adult male in a small family group of gorillas that included an adult silverback. In the wild, a gorilla of Joe's age would have emigrated from his natal group under pressure from the dominant silverback male; in this case, one might interpret Joe's escape attempts as efforts to ''emigrate'' from what was no longer an appropriate social group for his species. Anecdotal observations such as these suggest that housing animals in social groups that are not species-typical may also be stressful—though whether or not it is as stressful as keeping a social animal in isolation remains to be determined.

In addition to maintaining animals in social isolation or abnormal social groups, humans sometimes crowd too many animals into an enclosure, or remix groups repeatedly as a consequence of routine husbandry practices (such as veterinary checks or transport). Such practices also have documented ill effects on animal well-being. Crowding rhesus macaques results in significant increases in injuries due to increased fighting (Boyce et al., 1998). A similar effect of crowding on aggression is seen in farmed red deer (Blanc and Thériez, 1998). And crowding in gilts is associated with impaired sexual behavior and increased levels of plasma corticosterone (Hemsworth et al., 1986a,b,c). Stress resulting from social instability is hypothesized to explain mortality in several cases of captive dolphins (Waples and Gales, 2002). The mixing of unfamiliar pigs of similar ages and weights evokes severe aggression (Francis et al., 1996). And social instability deriving from repeated mixing reduces weight gain in group-housed female rats, and increases plasma corticosterone (Haller et al., 1999). Again, the effects of both crowding and social instability on common physiological and behavioral measures of stress are so well documented that both are often used as research paradigms to induce stress. Yet many

husbandry procedures in captivity involve crowding and the mixing of social groups, even if only temporarily. In nature, animals can retreat from agonistic encounters or avoid dominant conspecifics in potential conflict situations. In captivity, such conflict avoidance strategies may be impossible to employ. As suggested previously, the nature of social groups and the opportunities for conflict avoidance may be critical factors in the well-being of social species maintained in captivity.

4. Discussion: predictability, control, and boredom

What many if not all of the potential stressors reviewed above have in common is the inability of the captive animal to control them. Indeed, perhaps the greatest stressor in the lives of captive animals is their perceived or actual inability to control most aspects of their surroundings (Sambrook and Buchanan-Smith, 1997). Animals in captivity generally do not have control over what individuals serve as their social partners or their mates. They have little or no control over how much space they are able to put between themselves and other conspecifics, or between themselves and humans. They have little or no control over what kinds of food they are offered, nor when that food is made available. Nor are they generally able to control relevant environmental stimuli such as quantity, quality, and timing of lights, sounds, odors, or temperatures.

The importance of controllability in animal welfare is a complex subject, and one that is problematic for study (Sambrook and Buchanan-Smith, 1997). Nonetheless many investigators have argued that control is essential for animal well-being (e.g., Friend, 1991; O'Neill, 1989), and some data suggest a direct relationship between lack of control and behavioral and physiological operational definitions of well-being (for a review, see Mineka and Kelly, 1989). For example, hens that could control delivery of extra food and extra light showed less self-directed behavior than did hens without this control (Taylor et al., 2001). Rhesus macaques that could control the occurrence of loud, unpleasant sound showed lower cortisol levels than did macaques exposed to the same sounds without any ability to control them (Hanson et al., 1976). Similarly, dogs (Seligman et al., 1968) and rats (Seligman and Beagley, 1975) that had received inescapable shock and had subsequently "given up" all efforts to escape regained more adaptive behaviors for coping with the shock when they were trained to control it. Maier and Seligman (1976) call this giving up behavior "learned helplessness," and it is a phenomenon accompanied by a number of symptoms of chronic stress, including anorexia and subsequent weight loss (Rickards et al., 1997), inhibition of exploratory behavior (Wommack et al., 2004), and aberrant immune responses (Overmeier, 2002). If captivity affords animals little or no control over most aspects of their daily lives – particularly those that they may find stressful – then captive environments may also promote helplessness and the loss of adaptive coping strategies. If we have conservation of bio- and behavioral diversity among our husbandry goals, such passivity is an undesirable consequence of captivity. To the degree that captive environments afford animals little or no control over most aspects of their daily lives, they may be inherently stressful and also deleterious to long-term conservation efforts.

Another aspect of captivity that may be stressful to animals is its predictability (see review in Bassett and Buchanan-Smith, 2007). However, some studies have shown that animals given a choice will choose predictability over unpredictability, particularly over aversive events (Gliner, 1972). The impact of predictability or its lack appears to depend largely on the nature of the event or stimulus to be predicted (van Rooijen, 1991). Being able to predict the occurrence of events that are essential for survival (such as feeding or the opportunity to seek shelter) may be

essential for captive animal wellbeing, as some of the data reviewed above suggest. At the same time, however, the very predictability of routine husbandry schedules has been shown to stimulate undesirable behaviors (such as pacing), which can be eliminated or reduced by randomizing the timing of husbandry activities. Such observations have led some researchers to propose that the relentless predictability of routine husbandry and/or environmental stimuli present in captive environments in and of itself is stressful (Pepperberg, 2004; van Rooijen, 1991), because of the boredom that results.

It may be essential to introduce animals to a certain amount of unpredictability, if one of the goals of maintaining animals in captivity is conservation and eventual repatriation (Appleby, 1997). After all, novelty, unpredictability, and variability are all common features of the natural environment. To the degree that captivity affords animals little or no opportunity to manage important aspects of their lives (such as quality, quantity, and timing of food and water, choice of mates or other social partners, etc.), then captivity is also unlikely to provide animals with the kinds of experiences they will need to succeed outside of our care. To the extent, however that captive animals rely on routine to reduce anxiety about essential environmental features that they cannot control themselves (such as provision with food, water, and shelter), then failure to provide such assurances will surely be a cause of distress. The challenge, then, is to determine the optimal balance of variability and routine that is ideal for each species—and probably for each individual (for potential solutions, see Bassett and Buchanan-Smith, 2007). To some degree, we can rely on existing natural history data to guide us through this challenge; in many cases, however, the data most needed do not yet exist. Additionally, we may rely on careful observation and monitoring of species physiological and behavioral responses to elements of the captive environment for clues as to which (if any) of these elements may be causing stress at a given place and time.

Unfortunately as the literature reviewed above suggest, while there may be many behavioral and physiological indicators of stress, there are none that are unique to a given stressor in such way as to provide a clear diagnosis for the concerned caretaker. Many of the stressors reviewed above produce the same or very similar effects on animals, and some produce different effects in animals of different ages, sexes, or with different previous experience. This ambiguity makes such behavioral and physiological responses unreliable symptoms for troubleshooting a given captive situation; about all they may be able to tell us is that something is amiss, but alas—not precisely what is amiss. And paradoxically, many animals respond to stressors by exhibiting diametrically opposite suites of behaviors. That is, animals can respond to noise with increased locomotor activity or with paralysis. They can exhibit increased crypsis or increased investigatory behavior. They can become secretive or conspicuous. They can become silent or exhibit increased vocal activity. In short, an examination of the symptoms of stress will not generally help us to identify the source of the provocation. Rather, we will have to rely on a better understanding of species natural history and a fuller evaluation of *all* aspects of the captive setting when considering possible sources of stress in a given situation.

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