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COMPANION ANIMALS SYMPOSIUM: Environmental enrichment for companion, exotic, and laboratory animals¹

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ABSTRACT: Animal scientists have an extraordinary burden to promote the health and well-being of all animals in their care. Promoting species- or breed-appropriate behaviors through proper training and enrichment, regardless of animal housing, should be a paramount concern for all animal scientists working with exotic animals, laboratory animals, shelter animals, or privately owned pet animals. Developing ideal training and enrichment programs for any species begins with understanding basic behavior patterns and emotional systems of animals. The basic emotional systems in mammals have been extensively mapped; however, most of these studies are in the neuroscience literature and seldom read by animal science professionals. The emotional circuits for fear have been well documented through studies demonstrating that lesions to the amygdala will block both conditioned and unconditioned fear behaviors. Additionally, other core emotional systems including seeking (i.e., approaching

a novel stimulus), rage, panic (e.g., separation stress), play, lust (i.e., sex drive), and care (e.g., mother-young nurturing behavior) have been identified. More recent neuroscience research has discovered the subcortical brain regions that drive different types of seeking behaviors. Research to increase the understanding of the emotional systems that drive both abnormal and normal animal behaviors could greatly improve animal welfare by making it possible to provide more effective environmental enrichment programs. Enrichment devices and methods could be specifically designed to enable the expression of highly motivated behaviors that are driven by emotional circuits in the brain. The objective of this paper is to increase awareness of animal scientists to the field of neuroscience studying animal emotions and the application of that science to improve the welfare of captive exotic animals, laboratory animals, and pets with environmental enrichment.

Key words: animal welfare, companion animal, emotion, environmental enrichment, laboratory animal, nondomestic animal

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INTRODUCTION

Zoos, farms, and laboratories are often faced with public criticism regarding animal welfare. Animal scientists may be able to use neuroscience research to improve the understanding of animal behavior and improve environmental enrichment programs. Research in animal science, veterinary science, and ethology has

demonstrated that animals have behavioral needs. Research studies have demonstrated that certain innate behaviors, such as building a secluded nesting area for laying hens, rooting and chewing in pigs, and nest building in mice are highly motivated (Duncan and Kite; 1989; Olsson and Dahlborn, 2002; Day et al., 2008; van de Weerd and Day, 2009). Duncan (2004) was one of the first animal scientists to state that feelings or emotions were driving those behaviors. Unfortunately, most mainstream animal science literature does not discuss the underlying neural mechanisms that drive species-specific innate behaviors.

The neuroscience literature demonstrates that animal brains have emotional systems that are more specific than simply stating an animal exhibits psychological stress. The core emotional systems that serve as motivators for behavior are seeking (i.e., novelty seeking), fear, rage, panic (e.g., separation stress), lust (i.e., sex drive), caring (e.g., mother-young nurturing behavior),

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and play (Panksepp, 1998, 2005). This body of neuroscience literature may provide a background for animal scientists to better understand innate animal behaviors and implications for effective enrichment programs.

Good enrichment programs should provide animals opportunities for expressing behaviors driven by the positive emotional systems of seeking, play, and caring (Grandin and Johnson, 2009). Some examples of behaviors that are driven by these systems include foraging, grooming, play, and positive social interactions. The basic goals should be to increase positive emotions and decrease time that animals are subjected to fear, panic, and rage. Although it is impossible to eliminate all fear or short-term stress, it is essential to reduce conditions that promote constant fear or deprive opportunities for seeking.

A LOOK INTO THE EMOTIONAL LIVES OF ANIMALS

Distinct Brain Systems for Different Emotions

Experiments show clearly that animals have specific neurological systems for different emotions, such as fear and rage (Bard, 1928; Hess, 1957; Fernandez de Molina and Hunsperger, 1959; Panksepp, 1971; Davis, 1992). Jaak Panksepp was one of the first neuroscientists to introduce the concept of core emotional systems. He referred to them as fear, rage, panic (i.e., separation stress), and seeking (i.e., novelty seeking; Panksepp, 2005). More recent research has subdivided the seeking system in the rat brain into liking something and wanting something, the latter being the motivation to obtain it (Berridge et al., 2009). Some additional emotional systems are lust (i.e., sex), play, and caring (i.e., mother-young nurturing behavior; Panksepp, 2005). These emotional systems are all located in the subcortical parts of the brain and are similar in both anatomy and response to stimuli in people and other mammals (Fernandez de Molina and Hunsperger, 1959; Panksepp, 2003; Burgdorf and Panksepp, 2006). In the next section of this paper, research on each core emotional system and how it may influence animal well-being will be discussed.

Fear

Fear circuits in both animals and humans have been extensively studied and mapped (Davis, 1992; LeDoux, 2000). Fear is the most primitive emotion that motivates animals to avoid predators and other dangerous situations (LeDoux, 2000). Some of this literature was first introduced to animal scientists by Grandin (1997). All vertebrate animals can be fear conditioned (Davis, 1992). An example of fear conditioning would be an animal avoiding a place where it was subjected to a frightening stimulus. In a review, Davis (1992) cited

many studies that showed that electrical stimulation of the amygdala in animals triggers both behavioral and autonomic responses indicative of fear. In humans, electrical stimulation of the amygdala elicits feelings of fear (Chapman et al., 1954). Electrical stimulation of the amygdala in other mammals increases stress hormones, such as corticosterone (Redgate and Fahringer, 1973). If the amygdala is destroyed by lesioning, animals no longer learn to fear aversive stimuli (Davis, 1992). Kemble et al. (1984) noted that complete destruction of the amygdala had a taming effect on wild rats and decreased the size of their flight zone. More recent research has further mapped fear circuits and it is believed that the mammalian brain has 2 fear circuits (Rogan and LeDoux, 1996); one circuit is subcortical, which can trigger an instantaneous escape response and the second is a circuit through higher cortical areas, which takes longer for the brain to process, but provides more accurate information. The subcortical circuit enables an animal to survive because it will respond quickly to avoid danger (Rogan and LeDoux, 1996). Both circuits go through the amygdala, but the subcortical circuit bypasses the sensory cortex and goes directly from the thalamus to the amygdala (LeDoux, 1998).

Fear in Farm Animals During Handling and Restraint. Restraining and handling cattle and sheep significantly increased cortisol concentrations over baseline and these increases occurred even in the absence of painful procedures (Mitchell et al., 1988; Grandin 1997). In many species used in the laboratory, handling for cage cleaning and other procedures increased corticosterone (Balcombe et al., 2004). The increase in stress hormones and behavior, such as struggling or attempting to jump out of handling facilities, may be due to fear because restraint does not cause pain.

Fear of Sudden Novelty. Suddenly exposing an animal to a novel experience can be a strong stressor (Moberg and Wood, 1982; Dantzer and Mormède, 1983). Sudden novel stimuli can cause both behavioral escape reactions and elevations in stress hormones. These reactions are likely due to activation of the fear circuits because fear will increase stress hormones (Redgate and Fahringer, 1973). Tame animals accustomed to handling, or those trained for veterinary procedures, have reduced blood concentrations of cortisol and other substances, including lactate, compared with animals forcefully restrained (Boandl et al., 1989; Phillips et al., 1998). Edwards et al. (2010) found that pigs with greater lactate concentrations jammed more frequently in a handling chute compared with pigs with decreased concentrations of lactate. It is likely that jamming is motivated by fear because the pig becomes behaviorally agitated.

Genetics and Measuring Fear in Livestock

The degree of fearfulness, referred to as reactivity or excitability, is also influenced by genetics. Some genetic

lines of animals are more reactive and less likely to explore novel new environments compared with others. Rats have been bred to have either low or high anxiety (Broadhurst, 1975) and poultry have been bred to exhibit low or high fear (Mills and Faure, 1991). In cattle, temperament is heritable (Fordyce et al., 1988). Genetic differences in fearfulness in cattle are determined by utilizing temperament assessment methods, such as struggling in the squeeze chute or exit speed (Voisinet et al., 1997; Curley et al., 2006). In pigs, startle response caused by sudden foot stomping by a person was one of the most effective measures of detecting behavioral differences among different genetic lines (Lawrence et al., 1991). In poultry, fearfulness is measured with a tonic immobility test (Mills and Faure, 1986). Birds from more fearful genetic lines remain immobile for longer periods of time after being released from restraints (Mills and Faure, 1986).

Rage

Electrical stimulation of the hypothalamus and other subcortical areas causes aggression in cats and rats (Bard, 1928; Levison and Flynn, 1965; Panksepp, 1971). This is a separate subcortical system from fear; however, there are some overlapping areas of both fear and rage located in the amygdala of the cat (Ursin and Kaada, 1960). Stimulation of the hypothalamus of a cat with an electrode will activate the rage system and the cat will hiss and show the bodily postures of rage (Hess, 1957). When this research was originally conducted, it was referred to as sham rage, implying the rage was not real. In later experiments, hypothalamic stimulation led cats to discriminate between objects they attacked. Levison and Flynn (1965) found that hypothalamic stimulation caused most cats to attack anesthetized rats or stuffed rats, but they did not attack rat-sized blocks of Styrofoam. This indicates that the hypothalamus contains circuits that serve as drivers for real cat behavior.

Panic

Another emotional system that is distinct from fear circuits is panic or separation stress. This system is activated when a mother is separated from her offspring or an adult animal is separated from its herd mates (Herman and Panksepp, 1981; Panksepp, 2003). Isolating an animal can be a strong stressor and may activate the panic system. In quail, it was noted that the panic system and fear system were distinct (Mills and Faure, 1991). Those authors referred to panic as "social reinstatement" or "social motivation" (Mills and Faure, 1991). In normal wild quail, birds exhibit both high fear and high panic. These 2 emotional traits could be separated through selective breeding in quail (Faure and Mills, 1998) and researchers were able to breed 4 distinct genetic lines (i.e., high fear and high panic,

high fear and low panic, low fear and high panic, and low fear and low panic). Fear was measured by the tonic immobility test (Mills and Faure, 1986; Jones, 1987). Panic was measured with a moving strip of carpet that moved the test bird away from a cage that contained its flock mates. High panic birds spent more time walking against the motion of the carpet to stay close to their flock mates.

Seeking

Several scientists believe that all mammals and birds have a system for motivating an animal to orient and approach new things (Panksepp, 1998). Klüver and Bucy (1939) showed that complete removal of the amygdala and surrounding brain areas resulted in fearless monkeys that would examine every object in a strange room, whereas a monkey with an intact amygdala would not do this. The experimental monkeys had strong tendencies to attend to every visual stimulus. When fear was removed, the monkeys approached and sought out new things and did not engage in fear-motivated behaviors, such as climbing to higher locations.

The nucleus accumbens in the subcortex is activated when an animal seeks a reward (Ikemoto and Panksepp, 1999). Electrical stimulation of the nucleus accumbens led to a rat that was highly motivated to push a lever to obtain stimulation to this part of the brain (Olds, 1977). Reynolds and Berridge (2008) mapped the nucleus accumbens of rats. The extreme rostral tip always turned on appetitive behavior and the extreme caudal tip caused fear. The entire middle section had a mixture of locations that could trigger either appetitive seeking or fearful responses. The area devoted to the seeking response expanded when rats lived in a safe environment and it became smaller when the rats were exposed to stressful environments produced by loud music and bright lights (Reynolds and Berridge, 2008). Stimulation of one area activated approach behavior, whereas another area activated fear behavior (Faure et al., 2008). Therefore, the nucleus accumbens can either go into seek (i.e., appetitive behavior) mode or fear mode. Possibly, this same system explains the following behavior in cattle. They will approach a still novel person, sniff, and lick; however, if the person suddenly moves, the rapid movement causes them to startle and jump away. If the person remains still, the cattle will approach again. The cattle appear to be exhibiting an alternation between seek and fear (Grandin, 1997).

Smith and Berridge (2007) and Berridge et al. (2009), have further analyzed the appetitive seeking system and discovered that wanting something can be separated from liking something. Rats will lick their lips when they like a sweet substance. Wanting was measured by food intake, whereas liking was measured by observing licking behavior. Berridge et al. (2009) concluded that liking is due to the activity in opioid sites and dopamine sites were dedicated to wanting.

Both rats and mice have been bred to be either high novelty seekers or low novelty seekers, and Dellu et al. (1996) reported that genetics has an effect on the attraction of an animal to new things. The high-seeking rodents have greater dopaminergic activity in the nucleus accumbens (Dellu et al., 1996).

Play

Play behavior is driven by subcortical brain systems. Juvenile rats still play even after the cortex of the brain is removed (Panksepp et al., 1994). Many different species of animals exhibit play behaviors (Brownlee, 1954; Crowell-Davis et al., 1987). A possible evolutionary purpose of play is to train the motor skills of young animals and help them to cope with unexpected events (Špinka et al., 2001). The duration and bouts of play behaviors in animals housed under different conditions should be measured. The play system is still poorly understood and more research is needed.

Other Positive Emotional States

In many settings, it is not possible to measure caring behavior in animals that are housed in zoos or used in research because they are not permitted to breed. However, positive nurturing behavior interactions such as grooming between animals can be measured. Other behaviors used as indicators of a relaxed state are cud chewing in ruminants, self-care behaviors such as nose-licking in cattle, and preening in birds. Some of these behaviors may be driven by the brain systems that Panksepp (2005) refers to as caring.

Emotional Systems and Environmental Enrichment

Different types of abnormal behavior, such as bar biting in sows or stereotypic digging in gerbils, may be driven by different core emotional systems. If people caring for animals can determine what emotional system is driving an abnormal behavior, it may make it possible to design more effective environmental enrichments because the right enrichment would reduce the motivation to keep performing an abnormal behavior. Newberry (1995) stated that environmental enrichments should improve the biological function of the animal, and that appropriate endpoints should be measured after application of enrichments. The provided enrichment should prevent abnormal behavior or allow an animal to engage in more normal behaviors (Newberry, 1995).

Behaviors that are driven by the fear circuits are highly motivated, and environmental enrichments that prevent constant activation of these behaviors improve well-being. Gerbils dig stereotypically regardless of amount of substrate supplied until an adequate hiding cover or burrow is provided in the enclosure (Wieden-

mayer, 1997). Even in the absence of a predator, gerbils continue to dig; therefore, this innate instinctual anti-predator behavior may be motivated by the fear system. The gerbil is motivated to get under cover. To separate the variables of the need for digging versus the need for cover, an artificial pre-made burrow was provided. Gerbils that had the pre-made burrow greatly decreased repetitive digging (Wiedenmayer, 1997).

Foraging behaviors may be driven by the seeking circuits. Pigs are highly motivated to chew and root. A small handful of straw provided daily to sows in gestation crates helped prevent repetitive bar biting (Fraser, 1975). Pigs prefer soft materials to chew on and root in compared with hard materials, such as chains (Grandin, 1989; van de Weerd and Day, 2009). Weaving in stabled horses can be decreased by providing the animal with either more varied feed or changes in stable design. Thorne et al. (2005) found that providing a variety of forage types in addition to hay decreased weaving. The typical stable of stalls with solid walls and a single open door had more weaving horses compared with stalls that allowed the horse visual access in multiple directions (Cooper et al., 2000). Compared with the gerbils, pigs and horses were not motivated by fear. Abnormal and repetitive behaviors in pigs and horses were reduced when they were given opportunities to satisfy the motivation to seek.

The neuroscience literature provides great insights into the emotional drivers of highly motivated behavioral needs in farm animals, companion animals, laboratory animals, and animals in zoos. An understanding of the emotional systems that drive behavior will make it possible to greatly improve animal well-being by providing environmental enrichments that activate the brain's reward systems and decrease activation of the fear, rage, or panic systems.

ENRICHING THE LIVES OF EXOTIC ANIMALS IN ZOOS

Neuroscience research should be used to enrich the lives of captive exotic animals, companion animals, and animals in laboratories. Managers of these facilities recognize the importance of environmental enrichment. Behavioral enrichment is often mistakenly equated with terms such as variety, diversity, or novelty. In the field of captive wild animal management, enrichment characterizes a wide range of dynamic processes applied for enhancing animal environments, specifically within the context of the behavioral biology and natural history of a species. The goal of environmental enrichment is to increase the behavioral choices of an animal and draw out species-appropriate behaviors, thus enhancing animal welfare (Mellen and MacPhee, 2001). There is need for more research to determine which emotional systems are responsible for driving different types of normal and abnormal behaviors.

The application of management techniques encouraging species-typical behavior is not a recent phenomenon

among animal care professionals, yet the zoo industry has witnessed significant expansion in the field beginning in the 1980s (Mellen and MacPhee, 2001). Not unlike the integration of animal health, reproduction, or nutrition sciences into exotic animal husbandry, the current application and systematic review of environmental enrichment practices has emerged from a series of anecdotal and informal experiments to being objectively based in disciplines of ethology, psychology, and animal science (Shepherdson, 1998).

The inherent value of enrichment to captive exotic animal welfare is recognized by both regulatory and professional organizations. Federal regulation of environmental enhancement to promote psychological well-being of nonhuman primates was adopted in 1991 (APHIS, 2006). To comply with USDA Animal and Plant Health Inspection Service (APHIS) regulations, nonhuman primates are the only nondomestic species for which a formalized program of environmental enhancement is required by these minimum acceptable standards. Institutions accredited by the Association of Zoos and Aquariums are required to have a formal written enrichment program that promotes appropriate behavioral opportunities for all species under their care (AZA, 2011). These professional industry standards recommend that an enrichment program be based on current knowledge of species biology, and include a process of planning and approval to ensure animal safety, record-keeping, and assessment. Additionally, these accredited institutions must have a specific staff designated for enrichment program oversight, implementation, training, and interdepartmental coordination of enrichment efforts.

Potential enrichment techniques are as diverse as the behavioral repertoire of a species. As such, not all techniques are applicable to all species. Additionally, for practical reasons, and for animal and human safety, not all natural behaviors can be encouraged to their biological endpoint. For example, it would not be ethical to give lions live prey or to allow animals to produce excessive numbers of offspring. Current enrichment practices range in complexity from subtle changes in the physical or social environment of a species, or both, such that activation of fear and panic systems are reduced, to coordinated management training programs that may stimulate and activate the seeking system. Although such methods may be diverse, the efficacy of enrichment efforts is enhanced when approached systematically. Goal definition, program implementation, documentation of response criteria to facilitate objective evaluation, and continued refinement are hallmarks of a self-sustaining enrichment program (Mellen and MacPhee, 2001).

Modern naturalist zoo exhibit designs blend an array of organic and inorganic elements, and often immerse a particular animal species and visitors among an assortment of compatible plant and animals species, creating a range of opportunities for species-appropriate behaviors and opportunities to satisfy the motivation

to seek. These complex environments and enrichment techniques are not necessarily inconsistent with visitor recreation, wildlife conservation, and conveying an education message. In fact, methods based in enrichment implementation and evaluation have been used to enhance visitor experience among such complex animal environments and advance institutional goals (Kuhar et al., 2010).

Current research on environmental enrichment has focused on identifying, characterizing, and evaluating the relative importance of different environmental stimuli and evaluating effective means of their provision (Shepherdson, 1998). Mellen and MacPhee (2001) described several growth and development areas for captive animal enrichment programs, including 1) the development of proactive enrichment programs, rather than reactive methods; 2) plans to promote behaviors and activity patterns typical of the species; 3) objective assessment of methods and programs through the application of traditional behavior data collection methods; and 4) promoting accountability for enrichment programs throughout all levels of animal management staff (Mellen and MacPhee, 2001).

Among zoo animal professionals, science-based enrichment is an inseparable component of captive wild animal husbandry and welfare, both of which are defined and guided by the natural history and biology of a species. Future research should use the framework of the core emotional systems to develop more effective enrichment.

IMPROVING THE LIVES OF LABORATORY ANIMALS THROUGH ENRICHMENT AND TRAINING

The use of laboratory dogs and cats is quite prevalent in the United States, with over 22,000 cats and 72,000 dogs being used for research in 2007 (USDA, 2008). Although many guidelines have been set forth with regard to humane care and adequate space by the USDA and Public Health Services, little in the way of enrichment guidelines has been instituted. The only enrichment guideline regards exercise of dogs; however, it is up to the institutional veterinarian to develop and monitor the plan. Furthermore, exercise is only required if the cage size is not 2 times the minimum required. For laboratory cats, no enrichment guidelines currently exist.

Defining animal well-being is often difficult and knowing what types of behaviors and physiological indices to measure has proven difficult. In the end, the goal of providing enrichment and training in a laboratory setting is to decrease stereotypic behaviors, prevent or reduce aggression, and make research procedures less stressful for the animals and the research staff. Because this is a laboratory setting, enrichment must meet certain guidelines (e.g., durable enrichment items that can be sanitized) and not interfere with research results (e.g., providing edible items to animals in nutrition studies).

Environmental enrichment can reduce activation of the hypothalamic-pituitary axis. When rats were housed individually, the provision of toys and nesting materials decreased corticosterone concentrations (Belz et al., 2003). Another study showed that dogs in an animal shelter had smaller salivary cortisol concentrations the day after they were taken out of their cage and interacted with a person for 45 min (Coppola et al., 2006). Both of these studies indicate that simple environmental enrichment strategies can decrease physiological measures of stress. More research is needed to determine if activities that would decrease the stimulation of panic (i.e., separation stress) and fear systems, or increase the stimulation of play and seeking systems would decrease physiological measures of stress in laboratory animals.

For dogs, one of the first areas of research evaluated cage sizes and stereotypic behavior. The research to date has been contradictory, with some researchers finding behavioral changes with cage size (Hetts et al., 1992), whereas others report no changes (Neamand et al., 1975; Campbell et al., 1988; Bebak and Beck, 1993). Hetts et al. (1992) reported that dogs were less active in smaller cages, spent more time in barrier manipulation within their cages, and had numerically greater incidence of stereotypic behaviors during observation. The small cages used by Hetts et al. (1992) were large enough to not require supplemental exercise to a dog ≤ 38 cm long. The length of the dogs used in this study was not provided, but beagles were used, which are commonly < 38 cm from nose to the base of the tail. Although they may have moved less due to the size of the cage, this did not appear to have detrimental effects on the health of the animal.

Pair housing laboratory animals has become common practice and researchers must get specific approvals to house animals singly. Positive benefits have been noted with pair and group housing of animals, but a paucity of literature exists on these benefits. There are benefits to housing dogs with other dogs, including reduced noise, increased human interaction, and reduction of unwanted behaviors (Hubrecht, 1995; Mertens and Unshelm, 1996; Duxbury et al., 2003). Hubrecht (1993) noted that dogs spent less time in repetitive behaviors when group housed compared with individually housed dogs, but the authors noted this could be due to a variety of variables. The group-housed dogs had larger cages to accommodate more dogs, had social interaction with other dogs, and the cages had different feeding systems. The group-housed dogs were fed from a hopper in the middle of the cage, which required each animal to spend more time retrieving and eating food than dogs that were individually housed and fed from a bowl. This likely stimulated foraging behaviors driven by the seeking system. There was also a large variation among dogs on time spent in repetitive behaviors (Hubrecht, 1993). Even less evidence exists in cats. Although, anecdotally, some feel it is important to house

laboratory cats in maternal lineage groups (Overall and Dyer, 2005), the published literature supporting this is lacking. Rescued shelter cats became more tense when group housed at tight densities of < 0.6 cats/m² (Kessler and Turner, 1999), but laboratory cats, raised in such an environment, may respond differently. The background and degree of socialization of a cat may affect how it will adapt to group living. Practical experience in both animal shelters and laboratories indicate that most cats adapt well to group living when they are provided with both hiding places and a variety of sleeping platforms at different heights, likely decreasing stimulation of panic and fear systems.

It appears that pair or group housing animals may be beneficial, but the idea of mimicking these results with conspecific exercise has also been evaluated. Clark et al. (1997) evaluated 40 dogs (10/group), either not removed from their cage or removed from the cage but not exercised, individually exercised, or conspecifically exercised in pairs. The authors noted numerical increases of stereotypic behaviors in exercised dogs, especially after 3 mo on the test, and all dogs were found to bark more over time, regardless of exercise treatment. They concluded that cage confinement did not affect physical health of laboratory dogs and did not prevent stereotypic behaviors. A second study noted no benefits of treadmill exercise on abnormal behaviors in dogs (Hetts et al., 1992). Therefore, it appears that exercise, either alone or with conspecifics, does not appear to help prevent or lessen stereotypic behaviors in dogs as was reported in pair or group housing dogs. A fruitful avenue of research would be to develop enrichment programs that could help prevent activation of the core emotional systems of panic and fear, while stimulating the activation of seeking, caring, and play. Research needs to be done where the variable of exercise can be separated from the variable of contact with people. It is possible that contact with people has an effect on the panic system and exercise does not.

Reports regarding benefits of inanimate enrichment (e.g., toys or bedding in cages) are dominated by anecdotal findings; however, a new study showed that enriched cages reduced alopecia induced by barbering in mice (Bechard et al., 2011). In studies where rats have to be housed singly, cage enrichments increased exploratory behaviors and other species-typical behaviors (Abou-Ismael and Mahboub, 2011). It is important to understand the function of the enrichment object being used, and the behavior attempting to be modified, as the behavioral function of an enrichment object can be different, depending on the species (Newberry, 1995). A controlled study evaluating inanimate enrichment items suspended from the top of the cage noted that dogs environmentally enriched played less, decreased time spent interacting with their kennelmate, decreased time chewing on cage furniture, and spent a numerically greater amount of time in repetitive behaviors (Hubrecht, 1993). Inanimate enrichment with cats

led to less time being inactive (de Monte and Le Pape, 1997). Interaction with the enrichment object (e.g., a tennis ball or wooden log) decreased dramatically within days, and was object dependent. The cats seemed to prefer the tennis ball compared with a wooden log. Research with pigs has shown that new objects are preferred (Grandin, 1989; van de Weerd and Day, 2009). It is possible that providing new and novel objects each day would help activate the seeking system. This is an area that needs more research.

Other types of enrichment devices used for laboratory animals include feeding enrichment toys (e.g., where the animal must work to extract the food from the object; Clarke et al., 2005; Schipper et al., 2008) and providing bedding (Eisele, 2001; Severson, 2007). Kirby (2008) used laser pointers to provide play and stimulation for cats. Cats will pounce on and chase the red dot of a laser pointer when it is moved around on the floor. These reports were either anecdotal in nature or the enrichment had no influence on stereotypic behaviors. It should be noted that other factors must be considered before providing inanimate enrichment to laboratory animals. Objects provided in the cage must be durable to withstand abuse from both the animals and regular sanitization. They must be changed regularly as needed and should be safe for the animal to use unsupervised. Additionally, especially with dogs, aggression may develop between dogs trying to protect their toys. It was noted that dogs spent 50% of their observed time guarding their toy and monitoring their surroundings when inanimate enrichment objects were provided to them (Hubrecht, 1993). Problems with aggression can be reduced by providing sufficient numbers of highly desirable toys. This prevents the animals from fighting over a limited number of resources. In primates, poor distribution of enrichment devices may encourage aggression (Honest and Marin, 2006). Therefore, care should be taken to prevent the emotional systems from shifting from seeking toward panic or fear, when enrichment devices and activities are applied to animal husbandry practices.

Spending time interacting with animals is known to be beneficial to humans, but can this also be beneficial to laboratory dogs and cats? This form of enrichment can include human socialization (e.g., play time, grooming, or training) and is the most time-consuming type of enrichment we can provide. In an animal shelter, these types of activities lessened cortisol concentrations (Coppola et al., 2006). It is well established that dogs especially are highly social creatures. Hetts et al. (1992) noted that dogs with limited conspecific and human interaction had the greatest incidence of stereotypic behaviors and had the greatest number of vocalizations during the observation period. Furthermore, stressful management practices with cats led to less time spent exploring, more time spent behind the litter pan, and increased urine and serum cortisol concentrations within 1 wk (Carlstead et al., 1993). Hubrecht (1993) noted no changes in abnormal behaviors or vocalization of

dogs that were socialized with humans; however, they decreased chewing on cage furniture.

More recent research has evaluated the influence of behavior enrichment, including human interaction through cognitive training sessions and outdoor walks, on brain function. It was noted that geriatric animals that were behaviorally enriched and fed a high anti-oxidant diet had decreased oxidative damage in the brain, which may improve learning and memory (Opii et al., 2008). Behavioral enrichment alone decreased neuron loss in the hippocampus, which is important in cognitive abilities (Siwak-Tapp et al., 2008). These studies included a multitude of behavioral enrichments; however, it is not clear if it was one type of enrichment or the combination that led to changes in the brain. There is a paucity of information on the benefits of training animals with regard to well-being. Training may help decrease stress during routine research procedures, including weighing, nail trimming, walking on a lead, or collecting a blood sample. Training has been used in shelters to increase rehoming rates and decrease relinquishments, as behavior problems are the most common reason animals are relinquished. Therefore, it may be beneficial to train laboratory dogs and cats that will be adopted at the end of studies. Research in other species, such as antelope and cattle, showed that training the animal to cooperate during veterinary procedures and frequent contact with people decreased a physiological measure of stress (Boandl et al., 1989; Phillips et al., 1998).

Enriching and training our laboratory dogs and cats may lead to improved animal well-being, but more research is needed in this area. Anecdotal reports suggest that providing enrichment and training can be highly beneficial. It is important to consider the sanitization requirements, the facilities available, the temperament of the animal colony, and research outcomes being measured before implementing an enrichment program. It should also be noted that animals appear to have a highly individualized response to enrichment and what works for one animal, may not work for another. Finding ways to minimize stress and stereotypic behavior should be of importance in animal facilities. Providing good housing conditions, conspecific contact, inanimate enrichment, and socialization with humans may help decrease unwanted behaviors, but more research is needed with objective measurements. Using the framework of the core emotional systems would help researchers to design experiments that could lead to more effective environmental enrichments. Any enrichment program must meet the needs of the research being conducted and the abilities of the staff. Instituting a system that is beyond the abilities of the facility, staff, and research program would certainly not be useful.

ENRICHING THE LIVES OF PETS

According to the most recent trends and statistics from the survey of pet owners by the American Pet

Products Association (APPA, 2011), more than 164 million dogs and cats are living in more than 62% of US households. Of those pet owners, almost one-half (49.7%) considered their pets to be family members. Additionally, an estimated 5 to 8 million companion animals enter US animal shelters annually (Shepherd, 2008). Data have indicated that behavioral issues and concerns are among some of the major causes of owner relinquishments of companion animals (Salman et al., 2000; Weng et al., 2006; Kim et al., 2009). Of the behavior problems identified, aggression (51%) and inappropriate elimination (43%) were reported as the main causes of relinquishments of dogs and cats, respectively (Salman et al., 2000). Patronek et al. (1996) reported that inappropriate cost expectations rank among the top risk factors for owner relinquishments of pets. Lack of veterinary care, owning a sexually intact dog or cat, inappropriate care expectations, inappropriate elimination, and lack of training were all factors that explained the greatest proportion of companion animal relinquishments to animal shelters (Patronek et al., 1996).

According to the most recent trends and statistics reported by the APPA (2011), an estimated \$50.8 billion will have been spent on pets in 2011, with food accounting for the greatest segment of spending (38%), followed by veterinary care (28%), supplies (22%), services (7%), and pet purchase or adoption costs (4%). These statistics demonstrate the strength of the human-animal bond, along with the fascination of our society with 2 members (i.e., canines and felines) of the order Carnivora. The figures also highlight the need to address the husbandry of companion animals in US households to decrease behavior problems and owner relinquishments to shelters. A better understanding of how the core emotional systems affect behavior may lead to research that could assist with decreasing behavior problems in pets.

As with captive exotic animals, livestock, and laboratory animals, dogs and cats also are captive animals living by the constraints of their human caregivers, whether they reside in a home environment or shelter. Keeping animals in captive, under-stimulating environments can induce unwanted negative behaviors when animals are not allowed opportunities to express natural behaviors or exercise normally (McMillan, 2002; Young, 2003; Overall and Dyer, 2005). Allowing dogs and cats opportunities to exercise has been shown to decrease oxidative stress, improve cognitive function, decrease the risks of cognitive decline associated with aging, and improve learning (Milgram et al., 2005; Opie et al., 2008).

In addition, public perception and concern of animal well-being and mental health has been gaining interest over the past couple of decades. In a study conducted by Wells and Hepper (1992), the environment of a dog in a shelter had a significant influence on the preference of a subject in dog selection at the time of adoption.

Dogs photographed with toys were selected 95% more frequently than dogs photographed without toys.

Application of environmental enrichment for any species can only be accomplished when the natural history and behavior of those species are well understood. To apply environmental enrichment to companion dogs and cats, their species and breed-specific normal behaviors should be considered (Overall and Dyer, 2005; Overall et al., 2005; Ellis, 2009). In their basic taxonomy, both cats and dogs are in the order Carnivora. Many of their species-specific behaviors are similar to their wild counterparts.

Species-specific behaviors of the cat are very similar to those of its ancestor, the African wildcat (*Felis silvestris lybica*) and to free-ranging cats. Some of these shared behavioral patterns include social family rankings, elimination, and feeding behaviors (Overall and Dyer, 2005; Overall et al., 2005). Understanding these normal behaviors can assist owners in developing a home environment that allows cats to demonstrate normal behaviors without those behaviors becoming problematic, thus leading to owner relinquishments. For example, altering substrates in litter pans and cleaning litter pans frequently, can decrease the occurrence of inappropriate elimination patterns (Overall et al., 2005). To provide more natural opportunities to demonstrate feeding behaviors, interactive food toys can be used that cats must interact with to obtain food (Overall and Dyer, 2005; Overall et al., 2005; Ellis, 2009). Sensory stimulating enrichment can be developed with the use of water fountains, access to outdoor windows, pheromones and scents, and herbs such as catnip (Ellis, 2009). This type of enrichment application may stimulate the seeking system of the cat.

When considering the natural history of the dog, breed must be considered. Currently, over 150 different dog breeds are the direct result of human domestication and breeding programs. These breeds were developed by selecting for very specific physical and behavioral characteristics (Vilà and Leonard, 2007). These specific behavior characteristics may be better understood if they are conceptualized within the framework of the core emotional systems. There may be genetic differences in the strength of different core systems. For example, one dog may be a high seeker and another one a low seeker. The high seeker is motivated to constantly chase a ball and the low seeker is content to have a more sedentary life. Many of the behavioral characteristics were selected for, because the breed of dog served a particular role for humans, such as herding livestock or ridding barns of pests. Today, pet dogs often do not partake in the activities of their ancestors; however, those selected behavioral characteristics still remain. Pet dogs are often being asked to live under contradictory demands from their human care-takers as a result of misunderstood normal breed-specific behaviors, such as the Border Collie that herds small children or the Jack Russell terrier that digs up the flower bed. When those behaviors

are looked at for what they are, both are normal behaviors for these breeds. Unfortunately, they are expressed at inappropriate times. It is necessary to understand the biology of dog behavior to provide opportunities for dogs to express their normal behaviors in appropriate situations (Mugford, 2007). Dog owners can participate in many active stimulating sport activities, such as agility, obedience, flyball, Treibball, herding, lure coursing, retrieve and field work, canicross, or Frisbee. In addition to the exercise component of these sports, the human handler must take an active role in the training, thereby building the human-animal bond. In addition, providing appropriate areas or containers for digging, can aid in reducing the occurrence of unwanted digging behaviors at inappropriate times or locations. It is feasible that any of the above-listed activities could potentially stimulate the reward systems in the brain (seeking) while reducing the activation of fear, panic, and rage systems, although this research has not been conducted. Several studies have demonstrated the effects of early environmental stimulation to canines in the form of con- and contraspecific socialization. Additionally, puppies enrolled in early socialization or training classes are more likely to remain in the home and not get relinquished (Patronek et al., 1996; Duxbury et al., 2003; Kobelt et al., 2003; Seksel, 2008).

Many pets are relinquished to shelters because they have developed behavioral problems with which owners can no longer live. Owners need to maintain not only the physical health of their pets, but their mental health as well. Providing for the mental health of pets through environmental enrichment before the development of behavior problems, may be a key factor for keeping pets in homes. Research on how the core emotional systems affect the behavior of pets may help reduce behavior problems. The concept of environmental enrichment should be viewed as a component of companion animal husbandry. Developing educational programs for promoting the use of environmental enrichment for pets is an outstanding outreach and teaching opportunity for animal science programs.

THE NEED FOR RESEARCH ON EMOTIONAL SYSTEMS

Less than 2% of today's US population has anything to do with animal production agriculture; therefore, young men and women of today are limited in their exposure to the animal world. Most of their experiences are limited to a dog, cat, or at most, a horse; or the virtual reality of Animal Planet and Walt Disney. Many youth today yearn to work with animals and, under the influence of the media, many seek to work with non-food animal species. Because of minimal animal experiences outside the home or virtual settings, youth gravitate toward a more anthropomorphic attitude when thinking and working with animals. These anthropomorphic tendencies have the potential to create more emotional responses when working and dealing

with animals. More people are viewing animals as part of the family and there is a greater public awareness of animal issues and welfare. This awareness will in part, drive the future of how animals are cared for and managed. Studies regarding the science of animal emotions will help provide a much better understanding of animal behavior and improve animal husbandry practices in animal agriculture, homes, shelters, laboratories, and zoological institutions.

SUMMARY AND CONCLUSIONS

The framework of the core emotional systems may provide both researchers and people who work with animals with insights into the motivations of animal behavior. This may provide information for designing experiments to improve environmental enrichment. The emotional systems of seeking, fear, panic, rage, lust, play, and caring are the likely drivers of many highly motivated behaviors. Hens are highly motivated to find a secluded nest box (Duncan and Kite, 1989). It is likely that this behavior is motivated by fear and it would have prevented the wild ancestor of the domestic hen from being eaten by predators. Studies in many species show that many animals are highly motivated to obtain materials for nesting or rooting (Olsson and Dahlborn, 2002; van de Weerd and Day, 2009). In primates, fighting is increased if enrichment objects are poorly distributed. When sufficient objects are available and they are distributed properly, aggression decreases (Honest and Marin, 2006). When environmental enrichment practices are applied correctly, animal husbandry and welfare increase; however, if poorly applied, enrichment practices also can be detrimental to animal welfare. There is a definite need for more research addressing the core emotional brain systems and their influence on species-appropriate behaviors and behavior patterns. When studies are being designed, researchers should consider the emotional system or systems that may be driving particular behaviors. Developing a greater understanding of the core emotional systems in the brain and their influence on animal behavior will enhance animal husbandry practices across taxa.

LITERATURE CITED

- Abou-Ismaïl, U. A., and H. D. Mahboub. 2011. The effects of enriching laboratory cages using various physical structures on multiple measures of welfare in singly-housed rats. *Lab. Anim.* 45:145–153. doi:10.1258/1a.2011.010149.
- APHIS (Animal and Plant Health Inspection Service). 2006. 9 CFR § 3.81. Environment enhancement to promote psychological well-being. Pages 83–85. Accessed Sep. 27, 2011. http://edocket.access.gpo.gov/cfr_2011/janqtr/pdf/9cfr3.81.pdf.
- APPA (American Pet Products Association). 2011. 2009/2010 APPA Industry statistics and trends. National pet owners survey. Accessed Sep. 27, 2011. http://www.americanpetproducts.org/press_industrytrends.asp.
- AZA (Association of Zoos and Aquariums). 2011. AZA Accreditation Standards and Related Policies. Accessed Sep. 27, 2011. <http://www.aza.org/uploadedFiles/Accreditation/Accreditation%20Standards.pdf>.

- Balcombe, J. P., N. D. Barnard, and C. Sandusky. 2004. Laboratory routines cause stress. *Contemp. Top. Lab. Anim. Sci.* 43:42–51.
- Bard, P. 1928. A diencephalic mechanism for the expression of rage with special reference to the sympathetic nervous system. *Am. J. Physiol.* 84:490–515.
- Bebak, J., and A. M. Beck. 1993. The effect of cage size on play and aggression between dogs in purpose-bred beagles. *Lab. Anim. Sci.* 43:457–459.
- Bechard, A., R. Meagher, and G. Mason. 2011. Environmental enrichment reduces the likelihood of alopecia in adult C57BL/6J mice. *J. Am. Assoc. Lab. Anim. Sci.* 50:171–174.
- Belz, E. E., J. S. Kennell, R. K. Czambel, R. T. Rubin, and M. E. Rhodes. 2003. Environmental enrichment lowers stress responsive hormones in singly housed male and female rats. *Pharmacol. Biochem. Behav.* 76:481–486.
- Berridge, K. C., T. E. Robinson, and J. W. Aldridge. 2009. Dissecting components of reward: ‘Liking’, ‘wanting’, and learning. *Curr. Opin. Pharmacol.* 9:65–73.
- Boandl, K. E., J. E. Wohlt, and R. V. Carsia. 1989. Effect of handling, administration of a local anesthetic, and electric dehorning on plasma cortisol in Holstein calves. *J. Dairy Sci.* 72:2193–2197.
- Broadhurst, P. L. 1975. The Maudsley reactive and nonreactive strains of rats: A survey. *Behav. Genet.* 5:299–319.
- Brownlee, A. 1954. Play in domestic cattle in Britain: An analysis of its nature. *Br. Vet. J.* 110:48–58.
- Burgdorf, J., and J. Panksepp. 2006. The neurobiology of positive emotions. *Neurosci. Biobehav. Rev.* 30:173–187.
- Campbell, S. A., H. C. Hughes, H. E. Griffin, M. S. Landi, and F. M. Mallon. 1988. Some effects of limited exercise on purpose-bred beagles. *Am. J. Vet. Res.* 49:1298–1301.
- Carlstead, K., J. L. Brown, and W. Strawn. 1993. Behavioral and physiological correlates of stress in laboratory cats. *Appl. Anim. Behav. Sci.* 38:143–158.
- Chapman, W. P., H. R. Schroeder, G. Geyer, M. A. B. Brazier, C. Fager, J. L. Poppen, J. L. Solomon, and P. I. Yakovlev. 1954. Physiological evidence concerning the importance of the amygdaloid nuclear region in the integration of circulatory function and emotion in man. *Science* 120:949–950.
- Clark, J. D., D. R. Rager, S. Crowell-Davis, and D. L. Evans. 1997. Housing and exercise of dogs: Effects on behavior, immune function, and cortisol concentration. *Lab. Anim. Sci.* 47:500–510.
- Clarke, D. L., D. Wrigglesworth, K. Holmes, R. Hackett, and K. Michel. 2005. Using environmental and feeding enrichment to facilitate feline weight loss. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 89:427–433.
- Cooper, J. J., L. McDonald, and D. S. Mills. 2000. The effect of increasing visual horizons on stereotypic weaving implications for the social housing of stabled horses. *Appl. Anim. Behav. Sci.* 69:67–83.
- Coppola, C. L., T. Grandin, and R. M. Enns. 2006. Human interaction and cortisol: Human interaction and cortisol: Can human contact reduce stress in shelter dogs? *Physiol. Behav.* 87:537–541.
- Crowell-Davis, S. L., K. A. Houpt, and L. Kane. 1987. Play development in Welsh pony (*Equus caballus*) foals. *Appl. Anim. Behav. Sci.* 18:119–131.
- Curley, K. O., J. C. Paschal, T. H. Welsh, and R. D. Randal. 2006. Technical note: Exit velocity as a measure of cattle temperament is repeatable and associated with serum concentration of cortisol on Brahman bulls. *J. Anim. Sci.* 84:3100–3103.
- Dantzer, R., and P. Mormède. 1983. Stress in farm animals: A need for reevaluation. *J. Anim. Sci.* 57:6–18.
- Davis, M. 1992. The role of the amygdala in fear and anxiety. *Annu. Rev. Neurosci.* 15:353–375.
- Day, J. E. L., H. A. Van de Weerd, and S. A. Edwards. 2008. The effect of varying lengths of straw bedding on the behavior of growing pigs. *Appl. Anim. Behav. Sci.* 109:249–260.
- Dellu, F., P. V. Piazza, W. Mayo, M. Le Moal, and H. Simon. 1996. Novelty seeking in rats—Biobehavioral characteristics and possible relationship with the sensation-seeking trait in man. *Neuropsychobiology* 34:136–145.
- de Monte, M., and G. Le Pape. 1997. Behavioural effects of cage enrichment in single-caged adult cats. *Anim. Welf.* 6:53–66.
- Duncan, I. J. H. 2004. A concept of welfare based on feelings. Pages 85–102 in *The Well-Being of Farm Animals*. G. J. Benson and B. E. Rollin, ed. Blackwell Publishing, Ames, IA.
- Duncan, I. J. H., and V. G. Kite. 1989. Nest box selection and nest-building behaviour domestic fowl. *Anim. Behav.* 37:215–231.
- Duxbury, M. M., J. A. Jackson, S. W. Line, and R. K. Anderson. 2003. Evaluation of association between retention in the home and attendance in puppy socialization classes. *J. Am. Vet. Med. Assoc.* 223:61–66.
- Edwards, L. N., T. Grandin, T. E. Engle, S. P. Porter, M. J. Ritter, A. A. Sosnicki, and D. E. Anderson. 2010. Use of exsanguination blood lactate to assess the quality of preslaughter pig handling. *Meat Sci.* 86:384–390.
- Eisele, P. H. 2001. A practical dog bed for environmental enrichment for geriatric beagles, with applications for puppies and other small dogs. *Contemp. Top. Lab. Anim. Sci.* 40:36–38.
- Ellis, S. 2009. Environmental enrichment: Practical strategies for improving feline welfare. *J. Feline Med. Surg.* 11:901–912.
- Faure, A., S. M. Reynolds, J. M. Richard, and K. C. Berridge. 2008. Mesolimbic dopamine in desire and dread: Enabling motivation to be generated by localized glutamate disruption of the nucleus accumbens. *J. Neurosci.* 28:7184–7192.
- Faure, J. M., and A. D. Mills. 1998. Improving the adaptability of animals by selection. Pages 235–263 in *Genetics and the Behavior of Domestic Animals*. T. Grandin, ed. Academic Press, San Diego, CA.
- Fernandez de Molina, A., and R. W. Hunsperger. 1959. Central representation of affective reactions in forebrain and brain stem: Electrical stimulation of amygdala, stria terminalis, and adjacent structures. *J. Physiol.* 145:251–265.
- Fordyce, G., R. M. Dodt, and J. R. Wythes. 1988. Cattle temperaments in extensive beef herds in northern Queensland. 1. Factors affecting temperament. *Aust. J. Exp. Agric.* 28:683–687.
- Fraser, D. 1975. The effect of straw on the behavior of sows in tether stalls. *Anim. Prod.* 21:59–68.
- Grandin, T. 1989. Effect of rearing environment and environmental enrichment on the behavior and neural development of young pigs. PhD Diss. University of Illinois, Urbana-Champaign.
- Grandin, T. 1997. Assessment of stress during handling and transport. *J. Anim. Sci.* 75:249–257.
- Grandin, T., and C. Johnson. 2009. *Animals Make Us Human*. Houghton Mifflin, Harcourt, New York, NY.
- Herman, B. H., and J. Panksepp. 1981. Ascending endorphinergic inhibition of distress vocalization. *Science* 211:1060–1062.
- Hess, W. R. 1957. *The Functional Organization of the Diencephalon*. Grune and Stratton, New York, NY.
- Hetts, S., J. D. Clark, J. P. Calpin, C. E. Arnold, and J. M. Matteo. 1992. Influence of housing conditions on beagle behaviour. *Appl. Anim. Behav. Sci.* 34:137–155.
- Honess, P. E., and C. M. Marin. 2006. Enrichment and aggression in primates. *Neurosci. Biobehav. Rev.* 30:413–436.
- Hubrecht, R. C. 1993. A comparison of social and environmental enrichment methods for laboratory housed dogs. *Appl. Anim. Behav. Sci.* 37:345–361.
- Hubrecht, R. C. 1995. Enrichment in puppyhood and its effects on later behavior of dogs. *Lab. Anim. Sci.* 45:70–75.
- Ikemoto, S., and J. Panksepp. 1999. The role of the nucleus accumbens dopamine in motivated behavior: A unifying interpretation with special reference to reward-seeking. *Brain Res. Brain Res. Rev.* 31:6–41.
- Jones, R. B. 1987. The assessment of fear in the domestic fowl. Pages 40–81 in *Cognitive Aspects of Social Behavior in Domestic Fowl*. R. Zayan and I. J. H. Duncan, ed. Elsevier, Amsterdam, the Netherlands.

- Kemble, E. D., D. C. Blanchard, R. J. Blanchard, and R. Takushi. 1984. Taming in wild rats following medical amygdaloid lesions. *Physiol. Behav.* 32:131–134.
- Kessler, M. R., and D. C. Turner. 1999. Effect of density and cage size on stress in domestic cats (*Felis silvestris catus*) housed in animal shelters and boarding catteries. *Anim. Welf.* 8:259–267.
- Kim, Y.-M., A. M. Abd El-Aty, S.-H. Hwang, J.-H. Lee, and S.-M. Lee. 2009. Risk factors of relinquishment regarding canine behavior problems in South Korea. *Berl. Munch. Tierarztl. Wochenschr.* 122:1–7.
- Kirby, H. 2008. Cat herding: Using laser pointers for the environmental enrichment and behavioral management of laboratory cats. *Tech Talk* 13:3.
- Klüver, H., and P. C. Bucy. 1939. Preliminary analysis of the function of the temporal lobe in the monkeys. *Arch. Neurol. Psychiatry* 42:979–1000.
- Kobelt, A. J., P. H. Hemsworth, J. L. Barnett, and G. J. Coleman. 2003. A survey of dog ownership in suburban Australia—Conditions and behavior problems. *Appl. Anim. Behav. Sci.* 82:137–148.
- Kuhar, C. W., L. J. Miller, J. Lehnhardt, J. Christman, J. D. Mellen, and T. L. Bettinger. 2010. A system for monitoring and improving animal visibility and its implications for zoological parks. *Zoo Biol.* 29:68–79.
- Lawrence, A. B., E. M. C. Terlouw, and A. W. Illius. 1991. Individual differences in behavioral responses of pigs exposed to non-social and social challengers. *Appl. Anim. Behav. Sci.* 30:73–78.
- LeDoux, J. 1998. *The Emotional Brain: The Mysterious Underpinnings of Emotional Life*. Simon & Schuster, New York, NY.
- LeDoux, J. E. 2000. Emotion circuits in the brain. *Annu. Rev. Neurosci.* 23:155–184.
- Levison, P. K., and J. P. Flynn. 1965. The objects attacked by cats during stimulation of the hypothalamus. *Anim. Behav.* 13:217–220.
- McMillan, F. D. 2002. Development of a mental wellness program for animals. *J. Am. Vet. Med. Assoc.* 220:965–972.
- Mellen, J., and M. S. MacPhee. 2001. Philosophy of environmental enrichment: Past, present and future. *Zoo Biol.* 20:211–226.
- Mertens, P. A., and J. Unshelm. 1996. Effects of group and individual housing on the behavior of kennelled dogs in animal shelters. *Anthrozoös* 9:40–51.
- Milgram, N. W., E. Head, S. C. Zicker, C. J. Ikeda-Douglas, H. Murphey, B. Muggenburg, C. Siwak, D. Tapp, and C. W. Cotman. 2005. Learning ability in aged beagle dogs is preserved by behavioral enrichment and dietary fortification: A two-year longitudinal study. *Neurobiol. Aging* 26:77–90.
- Mills, A. D., and J. M. Faure. 1986. The estimation of fear in domestic quail: Correlations between various methods and measures. *Biol. Behav.* 11:235–243.
- Mills, A. D., and J. M. Faure. 1991. Divergent selections for duration of tonic immobility and social reinstatement behavior in Japanese quail (*Coturnix coturnix japonica*) chicks. *J. Comp. Psychol.* 105:25–38.
- Mitchell, G., J. Hattigh, and M. Ganhao. 1988. Stress in cattle assessed after handling, after transport and after slaughter. *Vet. Rec.* 123:201–205.
- Moberg, G. P., and V. A. Wood. 1982. Effect of differential rearing on the behavioral and adrenocortical response of lambs in a novel environment. *Appl. Anim. Ethol.* 8:269–279.
- Mugford, R. A. 2007. Behavioural disorders of dogs. Pages 225–242 in *The Behavioural Biology of Dogs*. P. Jensen, ed. CABI, Oxfordshire, UK.
- Neamand, J., W. T. Sweeny, A. A. Creamer, and P. A. Conti. 1975. Cage activity in the laboratory beagle: A preliminary study to evaluate a method of comparing cage size to physical activity. *Lab. Anim. Sci.* 25:180–183.
- Newberry, R. C. 1995. Environmental enrichment: Increasing the biological relevance of captive environments. *Appl. Anim. Behav. Sci.* 44:229–243.
- Olds, J. 1977. *Drives and Reinforcements: Behavioral Studies of Hypothalamic Function*. Raven Press, New York, NY.
- Olsson, I. A. S., and K. Dahlborn. 2002. Improving housing conditions for laboratory mice: A review of ‘environmental enrichment’. *Lab. Anim.* 36:243–270.
- Opii, W. O., G. Joshi, E. Head, N. W. Milgram, B. A. Muggenburg, J. B. Klein, W. M. Pierce, C. W. Cotman, and D. A. Butterfield. 2008. Proteomic identification of brain proteins in the canine model of human aging following a long-term treatment with antioxidants and a program of behavioral enrichment: Relevance to Alzheimer’s disease. *Neurobiol. Aging* 29:51–70.
- Overall, K. L., and D. Dyer. 2005. Enrichment strategies for laboratory animals from the viewpoint of clinical veterinary behavioral medicine: Emphasis on cats and dogs. *ILAR J.* 46:202–215.
- Overall, K. L., I. Rodan, B. V. Beaver, H. Carney, S. Crowell-Davis, N. Hird, and E. Wexler-Mitchel. 2005. Feline behavior guidelines from the American Association of Feline Practitioners. *J. Am. Vet. Med. Assoc.* 227:70–84.
- Panksepp, J. 1971. Aggression elicited by electrical stimulation of the hypothalamus in albino rats. *Physiol. Behav.* 6:321–329.
- Panksepp, J. 1998. *Affective Neuroscience: The Foundations of Human and Animal Emotions*. Oxford University Press, New York, NY.
- Panksepp, J. 2003. Feeling the pain of social loss. *Science* 302:237–239.
- Panksepp, J. 2005. Affective consciousness: Core emotional feelings in animals and humans. *Conscious. Cogn.* 14:30–80.
- Panksepp, J., L. Normansell, J. F. Cox, and S. M. Sivi. 1994. Effects of neonatal decortication on the social play of juvenile rates. *Physiol. Behav.* 56:429–443.
- Patronek, G. J., L. T. Glickman, A. M. Beck, G. P. McCabe, and C. Ecker. 1996. Risk factors for relinquishment of dogs to an animal shelter. *J. Am. Vet. Med. Assoc.* 209:572–581.
- Phillips, M., T. Grandin, W. Graffam, N. A. Irlbeck, and R. C. Cambre. 1998. Crate conditioning of bongo (*Tragelaphus eurycerus*) for veterinary and husbandry procedures at Denver Zoological Gardens. *Zoo Biol.* 17:25–32.
- Redgate, E. S., and E. E. Fahringer. 1973. A comparison of pituitary adrenal activity elicited by electrical stimulation of preoptic amygdaloid and hypothalamic sites in the rat brain. *Neuroendocrinology* 12:334–343.
- Reynolds, S. M., and K. C. Berridge. 2008. Emotional environmental retune the balance of appetitive versus fearful functions in nucleus accumbens. *Nat. Neurosci.* 11:423–425.
- Rogan, M. T., and J. E. LeDoux. 1996. Emotion: Systems, cells, synaptic plasticity. *Cell* 85:469–475.
- Salman, M. D., J. Hutchison, R. Ruch-Gallie, L. Kogan, J. C. New Jr., P. H. Kass, and K. M. Scarlett. 2000. Behavioral reasons for relinquishment of dogs and cats to 12 shelters. *J. Appl. Anim. Welf. Sci.* 3:93–106.
- Schipper, L. L., C. M. Vinke, M. B. H. Schilder, and B. M. Spruijt. 2008. The effect of feeding enrichment toys on the behaviour of kennelled dogs (*Canis familiaris*). *Appl. Anim. Behav. Sci.* 114:182–195.
- Seksel, K. 2008. Preventing behavior problems in puppies and kittens. *Vet. Clin. North Am. Small Anim. Pract.* 38:971–982.
- Severson, L. 2007. Inexpensive idea for feline enrichment. *Tech Talk* 12:4.
- Shepherd, A. J. 2008. Results of the 2007 AVMA survey of US pet-owning households regarding use of veterinary services and expenditures. *J. Am. Vet. Med. Assoc.* 233:727–728.
- Shepherdson, D. J. 1998. Tracing the path of environmental enrichment in zoos. Pages 1–12 in *Second nature: Environmental enrichment for captive animals*. D. J. Shepherdson, J. D. Mellen, and M. Hutchins, ed. Smithsonian Institution Press, Washington, DC.
- Siwak-Tapp, C. T., E. Head, B. A. Muggenburg, N. W. Milgram, and C. W. Cotman. 2008. Region specific neuron loss in the aged canine hippocampus is reduced by enrichment. *Neurobiol. Aging* 29:39–50.

- Smith, K. S., and K. C. Berridge. 2007. Opioid limbic circuit for reward interaction between hedonic hotspots of nucleus accumbens and ventral pallidum. *J. Neurosci.* 27:1594–1605.
- Špinková, M., R. C. Newberry, and M. Bekoff. 2001. Mammalian play: Training for the unexpected. *Q. Rev. Biol.* 76:141–168.
- Thorne, J. B., D. Goodwin, M. J. Kennedy, H. P. B. Davidson, and P. Harris. 2005. Foraging enrichment for stabled horses: Practicality and effects on behaviour. *Appl. Anim. Behav. Sci.* 94:149–164.
- Ursin, H., and B. R. Kaada. 1960. Functional localization within the amygdaloid complex in the cat. *Electroencephalogr. Clin. Neurophysiol.* 12:1–20.
- USDA. 2008. Animal Care Annual Report of Activities: Fiscal Year 2007. Animal and Plant Health Inspection Service, Washington, DC.
- van de Weerd, H. A., and J. E. L. Day. 2009. A review of environmental enrichment for pigs housed in intensive housing systems. *Appl. Anim. Behav. Sci.* 116:1–20.
- Vilà, C., and J. A. Leonard. 2007. Origin of dog breed diversity. Pages 38–58 in *The Behavioural Biology of Dogs*. P. Jensen, ed. CABI, Oxfordshire, UK.
- Voisinet, B. D., T. Grandin, J. D. Tatum, S. F. O'Connor, and J. J. Struthers. 1997. Feedlot cattle with calm temperaments have higher average daily gain than cattle with excitable temperaments. *J. Anim. Sci.* 75:892–896.
- Wells, D., and P. G. Hepper. 1992. The behaviour of dogs in a rescue shelter. *Anim. Welf.* 1:171–186.
- Weng, H.-Y., P. H. Kass, L. A. Hart, and B. B. Chomel. 2006. Risk factors for unsuccessful dog ownership: An epidemiologic study in Taiwan. *Prev. Vet. Med.* 77:82–95.
- Wiedenmayer, C. 1997. Causation of the ontogenetic development of stereotypic digging in gerbils. *Anim. Behav.* 53:461–470.
- Young, R. J. 2003. *Environmental Enrichment for Captive Animals*. Blackwell Publishing Co., Oxford, UK.

References

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