

UNRAVELING THE BEHAVIORAL MECHANISMS
BEHIND CONTRAFREELoADING

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the dissertation of RAGEN MARIE TRUDELLE-SCHWARZ MCGOWAN find it satisfactory and recommend that it be accepted.

Chair

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UNRAVELING THE BEHAVIORAL MECHANISMS
BEHIND CONTRAFREELoADING

Abstract

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Contrafreeloading occurs when animals choose resources that require effort to exploit when identical resources are freely available. Though contrafreeloading is well documented across species, little is known about the mechanisms behind the development of this behavior. This dissertation encompasses three projects which provide new insights into contrafreeloading in three species: grizzly bears, chickens, and mice.

Two experiments were conducted with captive grizzly bears to assess information primacy as a theoretical foundation for foraging enrichment. Contrafreeloading was examined in response to concealed food. Bears spent more time manipulating devices that contained concealed food than devices without food, showing that they were motivated to explore concealed resources. Bears did not always consume extracted food suggesting that consumption is not an exclusive motivating factor of foraging behavior.

Three experiments were conducted examining food choice in domestic fowl. To better understand apparent sex differences in foraging tactics in this species, two experiments were conducted in which sex hormones were manipulated. Contrafreeloading behavior, based on level of preference for foraging on small food particles in the presence of larger particles, was

compared between treatments. In a third experiment, sex differences were investigated directly, comparing contrafreeloading among hens and roosters. Contrary to prediction, there was no effect of steroid treatment on contrafreeloading behavior. The behavior of roosters was consistent with predictions for energy maximization and hens showed variability in contrafreeloading tendencies.

Little is known about motivation in relation to contrafreeloading. A consumer demand approach was utilized, requiring mice to pay a ‘cost’ to gain access to foraging resources to assess the strength of motivation of mice to contrafreeload. Despite increasing costs, motivation remained high for accessing all resources provided. Mice were most strongly motivated to access a contrafreeloading opportunity and non-nutritious food items, suggesting that mice may actively seek opportunities to engage in behavior that allows for information gain in relation to unconventional resources.

These studies of contrafreeloading behavior demonstrate that, when housed in captivity with access to reliable, easily exploited food sources, animals may retain a seeking motivation that is adaptive under natural conditions, where survival is dependent upon finding food in an unpredictable environment.

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Dedication

This dissertation is dedicated to my mother who not only told me, but showed me, that anything is possible and to my father who encouraged me to discover and pursue my true passions in life. I thank you both for your love and support, and for sharing your intellectual curiosity with me.

CHAPTER ONE

LITERATURE REVIEW

Contrafreeloading occurs when animals choose resources that require effort to exploit when identical resources are freely available. Though the phenomenon of contrafreeloading has been documented in a wide variety of species in captivity (see Osborne 1977 and Inglis et al. 1997 for reviews), little is known about the development of this behavior. Hypotheses for the occurrence of contrafreeloading run the gambit from ‘boredom in captivity’ to evidence of a ‘behavioral need’ to express foraging behavior. An apparent contradiction to the basic tenets of optimal foraging theory, contrafreeloading may be an artifact of captivity. Alternatively, it may represent an adaptive form of exploration where animals seek information about alternative food sources by sampling. This chapter will set the stage for three studies described within this dissertation by highlighting relevant aspects of the literature and identifying areas where questions relating to contrafreeloading remain unanswered. A brief introduction to optimal foraging theory paves the way for a review of the current hypotheses and theoretical framework used to explain the contrafreeloading phenomenon. Specifically, contrafreeloading will be discussed in terms of ‘behavioral needs’, ‘information primacy,’ ‘seeking’ motivation and its potential application to environmental enrichment of captive animal habitats.

Optimal foraging theory: what should the ideal animal do?

Optimal foraging theory employs the frameworks of adaptation, economics and decision theory to predict the behavior shown by an “optimal forager,” that is, an animal with perfect ability to maximize reward (MacArthur & Pianka 1966). Developed with natural selection in mind, the

underlying principle for the notion of an optimal forager is that if animals choose foraging strategies that maximize their net energetic gain, then they will have improved chances of survival and greater opportunities to pass on their genes (MacArthur & Pianka 1966; Charnov 1976). These early models for the optimal forager made idealistic assumptions about animal cognitive capacities to explain the ability of animals to estimate patch quality and weigh energetic costs of seeking and acquiring food, with near perfect accuracy, to produce an optimal foraging strategy (Shettleworth 2001; Andersen et al. 2006). It is highly unlikely that a forager will ever possess perfect knowledge about its environment, especially as most habitats will fluctuate in resource availability and animals must, therefore, deal with variability (Stephens & Krebs 1986; Stephens 1993; Theil & Hoffmeister 2004).

According to the principles outlined in optimal foraging theory, animals should decide whether to forage at a particular patch by comparing the current profitability of the patch with the expected profitability of searching elsewhere in the habitat (Stephens & Krebs 1986). Expectations are created through foraging experience. Therefore, in order to reach optimum foraging potential an animal must be capable of determining and readily distinguishing patch quality within its environment. The literature demonstrates that, at least in birds and mammals, individuals are capable of making such discriminations (Caraco et al. 1989; Valone & Giraldeau 1993; Alonso et al. 1995; Alm et al. 2002; Kacelnik & Brunner 2002; Schaefer et al. 2003).

It is generally accepted that cognitive processes play an important role in making foraging decisions (Shettleworth 1998). Animals that are capable of acquiring and storing information about resources within their environments, and continually updating this information

through exploratory behavior, should be able to estimate patch profitability from expectations based on prior experience (Toates 1983; McNamara & Houston 1985, 1987; Kacelnik & Todd 1992; Cuthill et al. 1994). More recent foraging models incorporate measures of memory and decision processing by combining optimal foraging theory with theories of behavioral timing (e.g. 'Scalar Expectancy Theory'--Kacelnik & Brunner 2002), or utilize discrete choice models, to account for what and when animals hunt based on characteristics of the prey and non-consummatory 'satisfaction' from prey acquisition (Cooper et al. 2007). These models, nevertheless, make predictions about animal foraging decisions based on maximizing reward. While the behavior of individual animals inevitably departs to varying extents from that of model optimal foragers, optimal foraging theory is useful for predicting the foraging decisions of animals in variable scenarios (Stephens & Krebs 1986; Alm et al. 2002; Klaassen et al. 2006).

Contrafreeloading: reflection of a behavioral need?

Animals are not always optimizers and, in fact, may adopt strategies that are less rewarded or require more effort. Each decision an animal makes is influenced by a variety of internal and external factors and various models have been proposed to explain how behavior develops (Lorenz 1950; Baxter 1983; Hughes & Duncan 1988; see Jensen & Toates 1993 for a review). Some motivational models concentrate on the external stimuli that trigger behavior and draw on the assumption that appetitive behavior is only performed as a necessary step in achieving the resources essential for survival (e.g. Baxter 1983). In these models, the functional consequences of behavior are fundamental to its performance. In this sense, if an animal is housed in a setting where all of its physiological needs are provided for, the animal will have no need to express appetitive behavior (Baxter 1983). However, this is not always the case. In many captive

settings, the opportunity to perform appetitive behavior could be as valuable to an animal as the functional endpoints that result from the behavior (Duncan & Kite 1989; Haskell et al. 1996; Sherwin et al. 2004). Alternative motivational models acknowledge both internal and external stimuli that trigger behavior and highlight the notion that animals may be motivated to perform appetitive behavior itself apart from any functional consequences the behavior achieves (Lorenz 1981; Hughes & Duncan 1988).

Attempts to explain contrafreeloading have invoked the idea of ‘behavioral needs’ (Jensen 1963; Hughes & Duncan 1988; Gardner & Gardner 1988; Inglis et al. 2001; Lindqvist et al. 2002; Young & Lawrence 2003) whereby animals are motivated to act out specific behavior patterns even if the physiological needs served by the behavior are already fulfilled (Brambell et al. 1965; Hughes & Duncan 1988; Dawkins 1990; Duncan 1998). Despite some controversy as to whether ‘need’ is an appropriate use of terminology (Jensen & Toates 1993; Cooper 2004), it is generally accepted that animals possess motivations apart from acquiring the resources necessary for survival and reproduction (Hughes & Duncan 1988; Poole 1992; Morgan & Tromborg 2007). These ‘behavioral needs’ are largely controlled by internal motivators that are present regardless of the environment the captive animal is provided (Hughes & Duncan 1988). Thus, the performance of behaviors classified as ‘needs’ will persist no matter what type of resources are made available to the animal (Duncan & Kite 1989; Duncan 1998; Sherwin et al. 2004).

Behavioral sequences that have inspired discussion of ‘behavioral needs’ include those where vacuum behaviors occur in the absence of appropriate stimuli or in cases where animals perform seeming frivolous behaviors when the functional endpoints achieved by these behaviors

are already provided. For example, some hens will repeat the initial motions of a dust-bathing bout when there is no suitable substrate to complete this behavior and perform some elements of nest-building behavior even if a suitable intact nest is available to them (see Duncan & Hughes 1988 for a review; Duncan & Kite 1989; Widowski & Duncan 2000). There are many examples where appetitive feeding behavior persists in satiated animals (Morgan 1974). A captive animal that has quickly consumed adequate food to meet nutritional requirements may still be motivated to perform the appetitive components (e.g. searching, hunting or processing) that normally precede food consumption (Duncan 1998; Inglis et al. 2001). For example, satiated primates will readily forage through brush piles to locate hidden food (Chamove et al. 1982) and felids will exhibit hunting behaviors in the absence of any need to assuage hunger (Leyhausen 1979). Many animals will also perform seemingly unnecessary feeding behaviors when consumption of the food is not contingent upon such behaviors (Swaigood et al. 2003). For example, lion-tailed macaques have been observed to orally “peel” food items lacking protective casings (e.g. carrots) when such action is not necessary for consumption (Smith et al. 1989). These observations support the argument that animals may be strongly motivated to express the behavioral components involved in food acquisition and processing (Morgan & Tromborg 2007).

In the case of contrafreeloading, foraging behavior clearly persists even if animals are satiated (the physiological endpoint of foraging); therefore, one could argue that contrafreeloading is a reflection of a ‘behavioral need’ to express foraging behavior. However, it may be that the endpoint of this apparently suboptimal foraging strategy is not satisfaction of a physiological need for nutritive substance, but rather an unseen resource – information. An

apparent contradiction to the basic tenets of optimal foraging theory, contrafreeloading may be a form of exploration where animals seek information about alternative food sources by sampling.

Contrafreeloading: seeking information?

In a natural environment, animals face fluctuations in resource abundance and can potentially diminish the risk of starvation by gathering information about resources they might exploit in the future. To maintain an accurate perception of resource availability, an animal has to continually gather information, that is, an animal has to look for changes in its environment (Berlyne 1960; Mench 1998; Inglis et al. 2001). Following this line of thought, the incentive to gather information is present at all times, but superseded by other mechanisms when a need arises.

It has been suggested that contrafreeloading may reflect a motivation to seek information, which cannot be satisfied by mere consumption of resources (Jones & Pillay 2004). This idea is consistent with the concept that animals possess a seeking system, described by Panksepp (1998 pg. 145) as “foraging/exploration/investigation/curiosity/interest/expectancy/ SEEKING system” that leads animals to explore everything in their environment from “nuts to knowledge.” Rooted in the extended lateral hypothalamic corridor of the brain, stretching from the ventral tegmental area to the nucleus accumbens, this seeking system provides a neurological basis for exploratory behavior in vertebrates (Panksepp 1998; Inglis 2000). Electrical stimulation of this brain area in humans is accompanied by an intense feeling of interest about one’s surroundings (Heath 1963) and in rats stimulation of this area triggers vigorous sniffing, whisker twitching and other behaviors typically associated with exploration (Ikemoto & Panksepp 1994). Behavior that results from experimental manipulation of the seeking circuitry in the brain closely resembles the

normal sequences of appetitive behavior that come before consumption. In this respect, the seeking system may motivate animals to perform appetitive behaviors, regardless of whether the animal is experiencing a physiological need for an ultimate goal to be satisfied (Panksepp 1998; Spruijt et al. 2001; Jones & Pillay 2004). The brain regions associated with the seeking system are among the first to learn appetitive tasks (measured through action potentials) and the first to show excitement when this knowledge is recalled (Olds et al. 1972; Panksepp 1998).

Contrafreeloading may reflect a motivation for animals to seek out information about the quality and accessibility of different resources (Inglis 2000; Swaisgood 2007). Such a motivation would be evolutionarily adaptive, as it would ensure that an animal had the best possible information to alter its normal feeding behavior in response to environmental challenges (Hughes & Duncan 1988; Day et al. 1998; Inglis et al. 2001). Experimental manipulations of dopamenergic pathways in rats and baboons provide support for the suggestion that contrafreeloading is intimately related to the seeking system. Amato and colleagues (2006) found that repeated doses of the dopamine D2/D3 receptor agonist, quinpirole, facilitate contrafreeloading for water in rats and Foltin (2001) reported that administration of the dopamine agonist, amphetamine, increases food seeking behavior in baboons. Arousal of the seeking system is not suggested to activate an internal experience of reward but instead to excite an animal to explore its surroundings (Panksepp 1998).

It is logical for wild animals to be motivated to explore the environment and to seek opportunities to learn about potential food items. In captivity, however, animals are usually fed on a predictable schedule with little to no fluctuation in food abundance. In a captive

environment, the need for information about potential resources for future foraging endeavors is diminished, yet it is in these controlled environments that contrafreeloading behavior is readily observed. So the question remains; what do captive animals achieve from contrafreeloading?

Functional explanation for contrafreeloading: does knowledge increase fitness?

Experimental evidence suggests that animals find information gain in itself reinforcing (D'Amato 1974; Hagan & Broom 2004), an observation embodied in the concept of 'information primacy' (Woodworth 1958; Inglis 1983). Recently a centerpiece in functional explanations of contrafreeloading, the 'information primacy' theory of exploration predicts that animals will search for food in the presence of readily available food, and continually explore their surroundings even when these environments lack the resources needed by the animal at the time of exploration. 'Information primacy' equates to intrinsic exploration (Berlyne 1960), whereby animals explore in an inspective and inquisitive manner and not in search of a specific resource.

By taking an 'information primacy' approach in describing contrafreeloading, authors are working under the assumption that information gain is continuous and that persistent information gain increases an animal's fitness by increasing the chances of that animal satisfying its primary needs in the future (Inglis et al. 2001). Both food and information act as incentives determining an animal's foraging choices. Information-gathering should increasingly take precedence over food intake only as deprivation decreases (Inglis et al. 1997). Inglis and colleagues (1997, 2001) have embraced these predictions in a 'fuzzy model of contrafreeloading,' which considers three main variables (1) hunger – level of food deprivation, 2) uncertainty – degree of unpredictability or ambiguity associated with earned food, and 3) effort – work required to obtain earned food

relative to free food) in an attempt to explain contrafreeloading in terms of ‘information primacy.’ The model predicts a negative relationship between level of hunger and contrafreeloading, with satiated animals engaging in the most contrafreeloading. An inverted-u relationship is predicted between levels of uncertainty (i.e. novelty, ambiguity or unpredictability) surrounding earned food and contrafreeloading, and a negative relationship is predicted between high levels of effort needed to exploit earned food and contrafreeloading.

What do we ‘know’ about contrafreeloading in relation to information gain?

Experimental support for the information primacy hypothesis for contrafreeloading has come from domestic rodents and captive and domestic birds (Inglis & Ferguson 1986; Forkman 1991, 1996; Bean et al. 1999; Inglis et al. 2001; Lindqvist et al. 2002). Four main approaches have been considered to test the information primacy hypothesis for contrafreeloading: manipulating hunger level prior to experimental trials (Inglis & Ferguson 1986; Bean et al. 1999; Lindqvist et al. 2002); varying the usefulness of information to be gained by contrafreeloading (Forkman 1991); providing opportunities to assess patch quality without work (Forkman 1996; Bean et al. 1999); and ‘knowledge tests’ subsequent to bouts of contrafreeloading at multiple patches (Bean et al. 1999; Lindqvist et al. 2002).

Following motivational theory set forth by Woodworth (1958), who proposed that information gathering is a prevailing activity which is interrupted when need states (such as hunger) become intense, Inglis and Ferguson (1986) attempted to manipulate contrafreeloading behavior by varying food deprivation levels in starlings and found that increasing deprivation decreased the performance of contrafreeloading behavior. The same approach utilized later by

Bean et al. (1999) with starlings, and Lindqvist et al. (2002) with domestic and jungle fowl, yielded similar results. While these studies provide experimental evidence that hunger plays a role in the level of contrafreeloading behavior expressed, they do not provide solid support for the hypothesis that information gain motivates contrafreeloading.

In an attempt to tease out the effect of uncertainty on contrafreeloading in Mongolian gerbils, Forkman (1991) manipulated the level of predictability surrounding foraging patches by altering patch quality (concentration of food to filler) between experimental sessions. He observed that contrafreeloading was reduced when patches were highly unpredictable, attributing this finding to the limited usefulness of any information gained in surroundings expected to change rapidly (Forkman 1991). To further clarify the relationship between contrafreeloading behavior and information gain, Forkman (1996) designed a scenario where opportunities for assessing patch quality besides working for food were provided, with the hypothesis that foragers engage in contrafreeloading because they cannot gather information about resources by other channels. Forkman (1996) compared the choices gerbils made between free food and food sources that could or could not be assessed visually. As was predicted, when information about a food source can be inferred without work, the occurrence of contrafreeloading decreased (Forkman 1996). In considering these results, Forkman concluded that contrafreeloading only occurs in situations where information can be gained through working for food (Forkman 1996). Bean et al. (1999) found supporting results in a study using a similar experimental design with starlings, concluding that contrafreeloading is reduced when there are channels for gathering information aside from working (Bean et al. 1999).

Bean et al. (1999-starlings) and, later, Lindqvist et al. (2002-domestic and jungle fowl) tested whether animals use information gained during contrafreeloading bouts to make subsequent foraging decisions. The authors predicted that if birds are allowed to contrafreeload at foraging patches of different qualities (quantities of seeds high→low), then they should learn the location and contents of each patch and use this information in later ‘knowledge tests’ (Bean et al. 1999; Lindqvist et al. 2002). In both studies, the authors determined that if, after food deprivation, birds were tested in extinction with the best patch removed they would reliably chose the second best patch on first approach (Bean et al. 1999; Lindqvist et al. 2002).

To further investigate the effect of contrafreeloading on information gain, Bean and colleagues (1999) used food deprivation to vary the level of contrafreeloading expressed by subjects in order to test whether reduced contrafreeloading would result in limited information gain. Reductions in contrafreeloading behavior did not produce apparent reductions in learned information (Bean et al. 1999). By contrast, Lindqvist and colleagues (2002) provided evidence suggesting that lower contrafreeloading by domestic fowl than jungle fowl was associated with reduced information gain by the domestic fowl. They recognized, however, that this finding could be based solely on a breed difference in learning capabilities. Further examination of the level of information gained relative to the level of contrafreeloading performed is necessary to resolve conflicts within the literature. Perhaps limiting contrafreeloading experience, rather than reducing the level of contrafreeloading through food deprivation, would yield stronger results.

It may be, however, that levels of contrafreeloading do not correlate closely with levels of information gain. It could be that individuals performing low levels of contrafreeloading acquire

information more efficiently than individuals performing higher levels (Bean et al. 1999). An alternative is that animals sometimes contrafreeload for reasons other than information gain. For example, Amato et al. (2006, 2007) consider that contrafreeloading is compulsive-like behavior. They report that repeated application of the dopamine D2/D3 receptor agonist, quinpirole, elevates lever pressing by rats for access to water in the presence of a water bottle providing “free” water. This behavior persists over time, whereas according to the information primacy hypothesis, contrafreeloading could be expected to decline to low levels after learning of an operant task that always produces the same outcome.

What exactly do animals learn from contrafreeloading?

The term contrafreeloading is often used in relation to consumption of earned food in the presence of free food. If we accept the ‘information primacy’ hypothesis for contrafreeloading then we accept that knowledge acquisition is the primary function of contrafreeloading. If this is the case, then we must consider how we define information and what this means about how we define contrafreeloading. If contrafreeloading is represented by consumption, then the type of information being gained relates to the palatability, nutrient contents and food pay off value of the food choices. In this sense, by contrafreeloading animals gain information about food quality through consumption. If contrafreeloading is instead represented by the choice to work for food in the presence of readily available food, then the type of information gained relates to the skills necessary to exploit food resources. In this sense, by choosing to work for food when work is unnecessary, animals are gaining the knowledge to be able to exploit the resource in the future if it becomes necessary. Of course, these two notions are not mutually exclusive, as the only way an animal can consume earned food is to perform the necessary skills to acquire the food.

However, consumption may not be necessary for contrafreeloading. By choosing to work for food in the presence of the same food in free form, animals may gain the information necessary to exploit that resource in the future without actually consuming any food.

For wild animals facing fluctuations in food abundance in an unstable environment, intrinsic exploration may create situations in which there is an opportunity to acquire biologically useful information (Berylne 1960; Day et al. 1998; Inglis 2000). Intrinsic exploration may facilitate the identification of new food items (Day et al. 1998) by fulfilling a motivation for animals to seek information about originally novel stimuli. Following this line of thought, contrafreeloading may not only provide a means for animals to gather information about alternative food sources (Inglis and Ferguson 1986; Forkman 1993; Inglis et al. 1997), but may serve also as a behavioral mechanism for learning to distinguish food items from non food items.

Only two elements of information gain in relation to contrafreeloading have been examined in the previous literature: knowledge of food quantity (Forkman 1991; Bean et al. 1999; Lindqvist et al. 2002) and knowledge of patch location (Bean et al. 1999; Lindqvist et al. 2002). Our understanding of the type of information gained through contrafreeloading will only be further developed with careful experimental designs that look at the specific knowledge that animals gain through their choice to work for food; for example, the skills to acquire food and information about food quality such as food spoilage. Further insight into the types of information gained through contrafreeloading will aid in clarification of the defining terms of the behavior and help us to better understand the underlying motivations behind the behavior.

Motivation: how motivated are animals to perform contrafreeloading?

Little is known about motivation in relation to contrafreeloading behavior. Some level of motivation for the behavior exists, or it would not persist so readily in captive species; however, to date there have been no published experiments designed to test the level of motivation to perform contrafreeloading. Understanding motivation is fundamental to understanding the underlying principles of animal behavior (Sherwin et al. 2004). Motivation is difficult to measure directly and, therefore, must be inferred from behavior or physiology (Kirkden et al. 2003).

Behavioral approaches borrowed from human microeconomics are widely used to investigate the motivational tendencies of animals (Lea 1978; Dawkins 1983; Cooper 2004; Kirkden & Pajor 2006). A consumer demand approach, which requires an animal to pay a 'cost' to gain access to a resource, has proved useful for quantifying motivational strength for a broad range of species (e.g. broiler breeders-Savory et al. 1993; pigs-Matthews & Ladwig 1994; laying hens-Foster et al. 1997; mink-Cooper & Mason 2000; calves-Holm et al. 2002; rats-Ladewig et al. 2002; foxes-Hovland et al. 2006). Assorted methods for imposing costs on animals have been utilized including operant tasks such as pressing levers (e.g. Sherwin and Nicol 1996), pecking keys (e.g. Sumpter et al. 1999) and pushing panels (e.g. Holm et al. 2002), or more complicated behaviors such as squeezing through narrow gaps (e.g. Nicol 1987), traversing water (e.g. Sherwin and Nicol 1995), lifting weighted doors (e.g. Mason et al. 2001) or pulling rubberized chains (e.g. Hovland et al. 2006). By increasing the effort required to gain access to a resource, it is possible to estimate both the strength of motivation towards and, therefore, perceived importance of, that resource to the animal (Lea 1978; Dawkins 1990; Mason et al. 2001; Sherwin et al. 2004). When faced with increasing costs for accessing resources, animals will persist in

exploiting behavioral opportunities they perceive as important and cease efforts to exploit opportunities they perceive as unimportant. In this sense, ‘necessities’ continue to be attained despite increasing costs and ‘luxuries’ are only attained when costs are minimal (Dawkins 1990; Bubier 1996; Kirkden et al. 2003).

The application of consumer demand theory in assessing animal motivation is a method that is still being cultivated. A review of the literature divulges careful consideration and debate (e.g. Kirkden et al. 2003; Warburton & Mason 2003; Cooper 2004; Kirkden & Pajor 2006) as to which measures borrowed from human economics have valid application to studies of animal motivation. There are positive and negative attributes to each measure, in terms of practicality and interpretation, so it may be beneficial to take an inclusive approach by considering multiple measures of demand. These include measures that are derived from the construction of demand functions and measures associated with quantifying energy expenditure (Mason et al. 2001).

Demand functions are usually quantified by plotting the regression line relating the reinforcements gained (number or duration of visits to each resource) to the cost of gaining access to the resource plotted on log-log coordinates to provide a straight line. The time spent with a resource has commonly been used as a measure of consumption with which to construct demand functions or measure income elasticity (Dawkins 1983; Faure & Lagedic 1994; Matthews & Ladewig 1994; Sherwin & Nicol 1996). The absolute value of the slope (‘elasticity coefficient’) indicates the strength of motivation to access a particular resource (Lea 1978; Dawkins 1983). Resources that are important to animals will have elasticity coefficients closer to zero and less important resources will have elasticity coefficients closer to one. It has also been

argued that strength of motivation can be represented as the area (‘consumer surplus’) under the regression line (Mason et al. 2001; Holm et al. 2002). A greater area indicates a higher motivation for a resource across the range of costs studied. If slopes are equal, then a higher Y-intercept (‘intensity of motivation’) indicates that an animal is more highly motivated across a range of costs (Dawkins 1990; Mason et al. 2001; Sherwin et al. 2004). Two measures of effort can also be considered in evaluating the strength of motivation to obtain particular resources. Total expenditure is calculated as a rate of cost per unit time, and reservation price as the maximum price each animal is willing to pay to access a resource (Mason et al. 2001). Calculations of effort expended to reach each resource can be used to compare motivational strength between multiple resources.

Strength of motivation can be used to assess the importance of activities or resources that might improve captive housing conditions, because motivation is inherently linked to feelings of pleasure and aversion (Cabanac 1979; Warburton & Mason 2003). Animal welfare could be jeopardized if captive environments do not provide opportunities for the execution of the behavioral sequences that animals are strongly motivated to perform (Dawkins 1988; Morgan & Tromborg 2007), including both appetitive and consummatory components of complex behaviors (Hughes & Duncan 1988; Spruijt et al. 2001; Clubb & Mason 2003). Ensuring that captive environments provide the resources that allow animals to carry out favored activities is suggested to improve quality of life in captivity (Dawkins 1990; Cooper & Mason 2000). In this regard, an increased understanding of the underlying origins of contrafreeloading behavior could yield insight into important elements to consider in housing captive animals.

How can the contrafreeloading phenomenon be applied? Environmental enrichment

An increased understanding of the complex physical, social, and psychological lives of wild animals has spurred a movement towards higher standards for enrichment of captive animal habitats. Researchers and animal handlers alike recognize that provision of basic necessities alone is not enough to maintain a healthy animal and that environmental enrichment is a key aspect of animal welfare. The American Zoo and Aquarium Association provide the following working definition of environmental enrichment:

“A process for improving or enhancing animal environments and care within the context of the inhabitants’ behavioral biology and natural history. It is a dynamic process in which changes to structures and husbandry practices are made with the goal of increasing behavioral choices available to animals and drawing out their species-appropriate behaviors and abilities, thus enhancing animal welfare.” (AZA, 1999)

Environmental enrichment is most commonly defined in the literature as an animal husbandry principle designed to enhance captive animal care by identifying and providing the stimuli necessary for optimal well-being (Shepherdson 1998). Successful enrichment can be measured by an improvement in the biological functioning of captive animals as a result of modifications to their environment (Newberry 1995).

Recognition of the appropriate enrichment

There is a limited number of theoretically based guidelines for creating enrichment programs that improve animal welfare and maintain success throughout the lifetime of a captive animal. In many cases, enrichment devices often represent human preconceptions of what might constitute environmental enrichment (Newberry 1995; Jones et al. 1996; Tarou & Bashaw 2007), and may

be abstract objects of little biological significance to the species at hand. The way in which an animal responds to a captive environment will vary with its natural history (Carlstead 1996; Seidensticker & Forthman 1998). Animals have evolved in response to selection pressures of specific environments; therefore, it is important to consider the biological background and potential needs of the animal. For example, burrowing animals may seek out natural substrates in which to dig; arboreal animals may seek out trees or similar structures on which to climb and rest (Kreger et al. 1998); and animals that evolved in a semi-aquatic habitat may seek out opportunities to wade or swim (Mason et al. 2001).

Close examination of a species' evolutionary history and preferences in the field may prove to be essential in determining the environmental factors that are important in captivity (Brain 1992; Kreger et al. 1998; Poole 1998; Clubb & Mason 2007). Environments are comprised of many different elements each contributing to the overall ambiance. It may not be a specific component, but a combination of several components that is attractive to an animal. Thus, different environments could promote a similar level of welfare despite having differing characteristics (Newberry 1995; Newberry & Estevez 1997).

Before attempting enrichment, the specific aspects that are lacking in the environment must be determined. One aim in providing an appropriate captive environment should be to create facilities that enable an animal to perform activities similar in complexity to those that it performs in the wild (Poole 1998), keeping in mind that not all behaviors that are expressed in the wild are important in captive environments (Hughes & Duncan 1988). An obstacle in creating a suitable captive environment is the complexity of natural environments (Newberry &

Estevez 1997) where animals are presented with an assortment of choices on a regular basis. Therefore, it is extremely difficult to make definitive decisions on which specific aspects of a captive environment will be valuable to the inhabitants (Appleby 1997).

Satisfying the seeking system: unpredictability, novelty & exploration

Captive environments should include some element of unpredictability and novelty in order to provide an animal with the anticipated input of new information and to satisfy curiosity (Poole 1998). The opportunity to seek information through the investigation of novel aspects of the environment may be valuable for animals (Panksepp 1998; Mench 1998; Jones & Pillay 2004). Wood-Gush & Vestergaard (1991) demonstrated that pigs more readily explore a pen adjacent to their home pen if it contains a novel object rather than one familiar to them. Rats (Renner & Seltzer 1991) and chickens (Newberry 1999) will voluntarily leave their home area to enter an area where they can investigate a variety of novel objects. Novelty temporarily increases arousal and stimulates exploratory behavior, which can produce beneficial effects. For example, environmental enrichment devices that increase exposure to novelty during development have been successfully employed in both mammalian and avian species to modulate fear responses (Meehan & Mench 2002). This is evidenced by increased activity in novel environments (Renner 1987) and decreased fear response to novel objects (Jones 1982). Giving an animal control with respect to seeking and interacting with, or avoiding, novel stimulation may influence the effectiveness of enrichment (Mench 1998; Newberry 2000).

Provision of exploratory enrichment is important for animals that are motivated to gather information. Species that are generalists or that are adapted to environments that are highly

variable in resource availability may seek opportunities for exploration. According to Griffin (1991), an animal experiences consciousness if it subjectively thinks about objects and events. In this sense a conscious animal contemplates current situations, memories, or anticipations of future situations (Griffin 1991). This process allows animals to compare choices and decisions that the animal “believes” will achieve desired results or evade unpleasant ones (Griffin 1991). For some animals, it may be important to provide devices that can be manipulated for reward. Such devices might include tools, toys, food dispensers, or destructible objects that the animal can contemplate.

Food acquisition and intake in captivity often utilizes different behavior than that performed when feeding in the wild, because captive animals are usually provided with a more limited selection of food types than they would encounter in the wild. However, captive animals may still be motivated to perform feeding behaviors that have been shaped by natural selection (Newberry 1995; Swaisgood 2007). Methods to provide a more suitable food program could include varying the consistency of food, hiding food, introducing live food items to be hunted and caught, or other means by which to vary food presentation.

A strategy often employed is providing animals with the opportunity to work for food through finding, manipulating and extracting food resources. A wide variety of foraging devices that require an animal to work to obtain food is offered to both wild and domestic animals in captivity as a means to diversify foraging behavior (see Table 1 for a summary). Prolongation of foraging and feeding behavior has been proposed as a potentially meaningful and continually engaging method of enrichment (Newberry 1995; Lindburg 1998). However, it is important to be

aware that increasing foraging time represents only one aspect of natural feeding behavior, and species-specific food-acquiring behavior should also be encouraged (Young 2003). Feeding enrichments are often provided when the principles underlying their effectiveness are poorly understood. It is important to identify characteristics of stimuli that best evoke elements of the behaviors that animals are motivated to perform, and that are rewarding for them to perform (Fraser 1984; Van de Weerd et al. 2003).

The many stages of foraging are internally regulated by both physiological and psychological consequences (Panksepp 1998; Spruijt et al. 2001; Jones & Pillay 2004). Therefore, it is probable that an animal's motivation to forage will decrease only if the animal performs and experiences the consequences of both appetitive and consummatory components of feeding (Jones & Pillay 2004).

Reasons to provide enrichment

A body of literature exists which suggests that inadequacies in the captive environment may lead to the expression of abnormal behavior and negative psychological states such as stress, frustration and boredom (Mason 1991; Carlstead 1998; Poole 1998), and that environmental enrichment may reduce or prevent the development of these abnormal behaviors and negative psychological states. Changes in the environment, and the ways in which an animal reacts to those changes, can have profound and robust effects on the brain and the behavior of that animal (van Praag et al. 2000; Faherty et al. 2003). There is evidence to suggest that housing animals in an enriched environment compared to housing in a barren environment can induce a number of beneficial neurochemical, neuroanatomical and behavioral changes within the animal (Larsson et

al. 2002). If animals are motivated to gather information about their environments and are not provided opportunities to do so in captivity (e.g. forage for food or overcome challenges), frustration of this seeking motivation may lead to negative psychological states or undesirable behavior such as stereotyped pacing (Clubb & Mason 2003).

Abnormal behavior

Abnormal behavior is often used as an indicator of reduced welfare. However, the relationship between abnormal behavior, such as stereotypy, and welfare is uncertain (Mason 1991). Some behavior currently considered abnormal may, in fact, be adaptive in captivity, giving individuals performing the behavior a selective advantage over those who do not perform the behavior (Newberry 1995). Garner (2005) suggests that abnormal behaviors can be divided into two categories: maladaptive and malfunctional behavior. Maladaptive behavior occurs when a 'normal' animal is housed in an 'abnormal' environment (Garner 2005). In this regard, behaviors that are part of an animal's normal repertoire in the wild may not suit the captive environment. For example, infanticide in mice occurs in the wild when population densities are large and burrow systems become overcrowded. This behavior may happen in captivity if cages are overstocked with breeding females (Garner 2005). Malfunctional behaviors are a product of abnormal brain development or neurochemistry induced by factors in the captive environment. For example, isolation rearing can induce changes in brain development that lead to stereotypy (Garner 2005).

In a clinical definition, stereotypy is characterized by repetitive but purposeless and non-functional motor behavior, where movements appear to increase with stress, frustration and

boredom (DSM-IV 1994). It is necessary to examine the processes that control the performance of a stereotypy carefully in order to unravel the underlying motivation. There is evidence that stereotypies originate from behavioral patterns that are part of the animal's natural behavioral repertoire and that the processes that control normal behavior may also underlie these seemingly abnormal behaviors (Mason 1991; Wurbel et al. 1998).

The form of stereotypy contains information on its underlying motivation. The incidence of many oral stereotypies (i.e. bar biting in mice, cribbing in horses, sham chewing in swine) depends upon the motivational systems underlying feeding behavior (Lawrence & Terlouw 1993; Rushen et al. 1993). The feed provided may fulfill nutritional requirements but not satisfy the animals' motivation to perform feeding behaviors. Other stereotypies depend more on features of the physical environment (e.g., pacing in large carnivores, weaving in elephants and horses, route tracing in rodents and birds), suggesting that an inadequate housing system (e.g., insufficient space) lies at their origin (Wurbel et al. 1998; Clubb & Mason 2007).

It is hypothesized that stereotypy arises when animals are repeatedly motivated to perform a behavior but are kept in ways that do not allow the performance of all components of that motivated behavior. Preventing natural behavior patterns in animals can give rise to stress and frustration, and impair the development of brain regions that are involved in behavioral sequencing, thereby reducing the animal's ability to behave flexibly (Garner & Mason 2002; Garner 2005). If stereotypies do indeed originate as appetitive motivation, appropriate environmental enrichment might be a means of eliminating these behaviors by providing the stimulation the animal is seeking (Spruijt et al. 2001; Jones & Pillay 2004).

Negative psychological states

An inappropriate or suboptimal environment can lead an animal into negative psychological states, such as depression, fear, boredom or frustration. Chronic expression of these states can be considered detrimental to an animal's well-being.

Depression: The clinical definition of depression includes such characteristics as loss of interest or pleasure, reduced appetite leading to significant weight loss, and decreased energy, tiredness and fatigue (DSM-IV 1994).

Fear: Fear is a state resulting from perceived danger (Duncan 2000) and can be associated with exposure to novel stimuli.

Boredom: Boredom and apathy result from housing in unstimulating environments. Boredom is defined as a state resulting from chronic lack of opportunities for active interaction with the environment (Wemelsfelder & Birke 1997).

Frustration: Frustration is the state that arises when animals are prevented from performing behaviors that they are motivated to perform. This may be either by being physically blocked or psychologically inhibited from performing the behavior or because some key stimulus in the environment is missing (Duncan 2000). Signs of frustration include: displacement activities, vocalizations, aggression, over-grooming, stereotypy, apathy, and learned helplessness (Sherwin 2000).

Stress: Stress is defined by an extensive list of behaviors including signs of arousal or agitation, displacement activities, vocalizations, aggression, over-grooming, stereotypy, apathy, and learned helplessness (Sherwin 2000). In physiological terms, increased concentrations of hypothalamic-pituitary-adrenal (HPA) axis hormones, particularly corticosterone or cortisol, are used as indices of stress (DeVries 2002).

Chronic stress: Chronic stress has been demonstrated to lead to the following deficiencies: cardiovascular disease, suppressed immunity, ulcers, reproductive failure, dwarfism, depression, stereotypies and death (Mason 1998; Sapolsky 1998).

Problems arise when focusing enrichment efforts on alleviating negative emotional states, as these states cannot be measured directly. It is difficult to obtain concrete evidence that an enrichment device has replaced negative with positive emotional states, although recent work measuring ‘optimistic’ and ‘pessimistic’ tendencies in animals is promising (Matheson et al. 2007). If an animal’s welfare is regarded as good when positive affective states, such as pleasure, predominate over negative affective states such as stress (Spruijt et al. 2001), environmental enrichment should aim to activate the systems that are related to positive affect (Panksepp 1998; Jones & Pillay 2004). By increasing the appropriateness of enclosure design and environmental enrichments offered, and by allowing “pre-emptive instead of reactive access” to enrichment devices, we may be able to improve the welfare of many captive animal species (Clubb & Mason 2007).

Affective state: influence on decisions

A review of the literature on emotion reveals several studies suggesting that affective state may lead to cognitive bias. More specifically, information interpretation and processing could be biased by emotion. Humans demonstrate cognitive bias based on their emotional state. It seems that ‘happy’ people are more optimistic than ‘sad’ people when it comes to predicting the outcome of future events. Wright and Bower (1992) used human subjects to examine whether a person’s mood may directly affect his or her judgment of the uncertainty of a future event. Subjects were asked to report probabilities for personal and non-personal events while they were in an induced happy, neutral or sad mood. Consistently, ‘happy’ people reported more optimistic outcomes and ‘sad’ people reported more pessimistic outcomes; supporting the notion that depressed people tend to make negative judgments about events and provide unfavorable interpretations of ambiguous stimuli (Wright & Bower 1992).

This ‘optimistic’ vs. ‘pessimistic’ bias has also been demonstrated in laboratory animals. Harding and colleagues (2004) demonstrated that rats housed in highly unpredictable conditions (that induce a state characteristic of depression in humans—Willner 1997) display a similar “pessimistic” response bias. Using ambiguous stimuli to probe their subjects’ anticipation of positive or negative events, the authors found that rats in unpredictable housing show behavior indicating reduced anticipation of a positive event (Harding et al. 2004). The authors interpret their findings as evidence of a pessimistic response bias and suggest that this bias can be used as an indicator of affective state in animals, which could facilitate progress in animal welfare studies. Matheson and colleagues (2007) found similar results, with starlings housed in enriched

environments showing more optimistic responses to ambiguous stimuli than those housed in unenriched environments.

Effects of environmental enrichment on behavior

Enrichment and stereotypy

Carlstead & Seidensticker (1991) examined the behavior of a captive black bear, *Urus americanus*, in an attempt to understand the mechanism underlying the display of stereotypic pacing. During behavioral observations, the authors noted a seasonal difference in the expression of this behavior. In the early summer, the bear's pacing behavior was oriented away from the exhibit and was performed most frequently after feeding (Carlstead & Seidensticker 1991). By contrast, in the late summer and early fall, the bear's pacing behavior was oriented toward the exhibit and performed most frequently around feeding time (Carlstead & Seidensticker 1991). In comparing the seasonal effects on the bear's stereotypy to seasonal changes in the behavior of wild bears, the authors concluded that the stereotypic pacing was most likely generated from two main behaviors that could not be performed in the captive environment: mate seeking behavior, predominating in the late spring, and foraging behavior in the late summer and fall (Carlstead & Seidensticker 1991). In attempting to reduce the occurrence of stereotypic pacing in the spring, the authors placed bear odors in the enclosure. The introduction of bear odors to the habitat resulted in a reduction in pacing and increase in exploration and foraging behavior. In addition, hiding small food items in the exhibit during the fall almost completely eliminated pacing and replaced it with foraging (Carlstead & Seidensticker 1991). For wide-ranging species, the success of enrichments may be more related to their impact on ranging (Clubb & Mason 2007), general exploration or cognitive challenge (Meehan & Mench 2007) than on appetitive

components of behavior, specifically. While many functional questions about stereotypy remain, appropriate environmental enrichment can reduce stereotypy in captive animals (Carlstead 1998); therefore, investigating the factors associated with stereotypy helps to identify enrichment methods that are likely to reduce these types of behaviors.

Enrichment and stress

Lack of enrichment may lead animals to a state of anxiety. Sherwin and Olsson (2004) offered mice free access to a solution of Midazolam, an anxiolytic drug, and compared animals housed in unfurnished cages with animals kept in more spacious cages that were enriched with a nest box, a running wheel, cardboard tubes and nesting material. The unenriched mice consumed significantly more of the solution than the enriched mice, suggesting that more space along with enrichment made the enriched animals less anxious. Van de Weerd and colleagues (2002) came to a similar conclusion when assessing fear-related behaviors of mice kept in groups in small barren cages or in large cages furnished with gnawing blocks, climbing structures, a nest box and wood-wool. Boinski and colleagues (1999) used behavioral measures, along with plasma and fecal cortisol levels, to evaluate the effectiveness of toys and foraging enrichment provided to wild-caught brown capuchin monkeys held in captivity. The authors found cortisol levels to be higher during periods without enrichment than when enrichment was present (Boinski et al. 1999). In addition, increased cortisol levels during unenriched periods were correlated with an increase in the expression of abnormal behaviors including excessive grooming, self-mutilation, and stereotypy which the authors took as indicators of stress (Boinski et al. 1999). Reduction of abnormal behaviors and decreased cortisol levels during enrichment periods suggest that access

to a variety of toys and foraging enrichment devices reduces stress and enhances psychological well-being in captive capuchins.

Comparable results are evident for domestic animals housed in captivity. De Jonge and colleagues (1996) found that pigs reared in an unenriched environment showed delayed estrus, decreased weight gain, and a prolonged increase in cortisol levels after tethering compared to tethered pigs that had been reared in an enriched environment. Similarly, rabbits kept in a conventional cage system showed more restlessness, grooming, bar-gnawing, and timidity, and had elevated corticosteroid levels, compared to rabbits kept in an enriched cage system (Hansen & Berthelsen 2000).

Enrichment can also reduce and/or prevent the development of some self-mutilating behaviors and may be able to compensate for the effects of early experiences such as maternal separation. Meehan et al. (2003) found that foraging opportunities and increased physical cage complexity both prevented and reduced psychogenic feather picking by Amazon parrots. Provision of foraging substrates to chickens early in life also reduced the development of severe feather pecking, suggesting that it might reduce cannibalistic behavior later in life (Huber-Eicher & Wechsler 1997, 1998).

Many investigators suggest that allowing an animal to have some aspect of control over its environment is a critical element for improving animal welfare (Coe 1995; Markowitz & Aday 1998; Owen et al. 2005; Ross 2006). Providing animals with choices is a simple method by which to offer an element of control in a captive environment. This may include the choice to

turn on or off various sensory stimuli (e.g. Hanson et al. 1976), enter specific areas of an enclosure (e.g. Ross 2006), or the opportunity to choose between food items requiring various levels of effort for consumption and engage in contrafreeloading. Not surprisingly it has been demonstrated that being able to influence one's environment is rewarding (e.g. Markowitz & Line 1991; Hagen & Broom 2004) and that loss of such control increases stress (Overmier et al. 1980). Thus, providing the opportunity for an animal to have control over how it feeds may improve welfare.

Effects of environmental enrichment on the brain...

Morphological changes in the brain

Recent studies are delineating effects of environmental enrichment on neural plasticity in the mammalian brain (van Praag et al. 1999, 2000; Faherty et al. 2003). In one such study, Faherty and colleagues (2003) examined the effects of various components of an enriched environment on neuronal change in the mouse brain. Enriched environments resulted in animals with a significant increase in total cell volume, total dendrite length, and dendritic branching in the hippocampus CA1 region (an area functionally associated with learning and memory) compared with animals in an unenriched environment (Faherty et al. 2003). No differences were observed in the pyramidal cells of the motor cortex and the spiny neurons in the striatum, which are associated with motor activity, suggesting that changes in the CA1 and dentate gyrus morphology resulted from alterations in the animal's environment and not solely from an increase in motor activity. Because alterations in neural morphology occurred only in animals that were reared in a complex environment, it appears that continual change, novelty, and complexity, rather than physical activity alone, are important determinants of the environmental

enrichment effect on neural plasticity (Faherty et al. 2003). Nevertheless, motor learning, in addition to social and spatial learning, may contribute to significant morphological changes, including addition of synapses and dendrite outgrowth, in the brains of animals housed in enriched environments (Kleim et al. 1996; van Praag et al. 2000; Faherty et al. 2003).

Functional changes

It is important to consider the functional significance of neuronal change. Increased dendritic branching in the hippocampus is hypothesized to be associated with improved performance in learning tasks, spatial memory, and ability to habituate quickly to novel situations (Mohammed et al. 1990). Animals housed in unenriched environments may be more prone to addiction or perseverative behaviors than animals housed in enriched environments. Interestingly animals that are reared in an impoverished environment show more tendencies toward contrafreeloading behavior than animals reared in an enriched environment. Cobum & Tarte (1976) reared rats in either an impoverished or enriched environment and then housed the rats in an operant chamber with a contrafreeloading paradigm. The rats were not trained to lever press and free pellets were always available from a dish in the chamber. Cobum & Tarte (1976) found that the rats reared in the impoverished environment contrafreeloaded significantly more than the rats reared in the enriched environment. In addition, the rats reared in the unenriched environment seemed more motivated to work, making 57 times as many bar presses as the enriched animals (Cobum & Tarte 1976).

After their contrafreeloading trials, Coburn & Tarte (1976) removed the free food source from the experimental chambers and left rats housed with only the option to work for food.

Behavioral differences between the two groups were astounding. Whereas the impoverished group continued to lever press to obtain pellets and maintained their previous level of food consumption, the enriched group made few lever presses until almost 18 hours after food removal and took more than 3 days to approach previous consumption levels (Coburn & Tarte 1976). The authors took these results to indicate that the enriched rats did not learn the response task in the presence of free food, since they made very few bar presses during the contrafreeloading trials.

Rats raised in impoverished environments demonstrate increased impulsivity (Wood et al. 2006) and increased response to incentive stimuli such as food rewards (Rose et al. 1986) and drugs (Bardo et al. 2001). It has been suggested that contrafreeloading behavior may result as a side effect to alterations in the dopaminergic transmission pathways (e.g. Amato 2006). There is evidence that environmental enrichment can slow dopamine uptake in some areas of the brain (e.g. Zhu et al. 2005); therefore, animals reared in unstimulating environments may be significantly more sensitive to dopamine than animals reared in enriched environments. Several areas associated with dopamine reception are altered by environmental enrichment, including the prefrontal cortex and nucleus accumbens (Wood et al. 2005; Zhu et al. 2005). The same areas are associated with impulsivity (Cardinal et al. 2001; Jentsch & Taylor 1999) and learning (Foster 2001; Kelley 2004). Alterations in these functional areas of the brain may contribute to the behavioral differences that are observed between animals housed in enriched and standard housing conditions. It has also been suggested that reductions in compulsivity in enriched animals result from opportunities to “cultivate” the seeking system (Bardo 1996), whereas

animals that have had very little exposure to novelty may be super-sensitive to this stimulation and react in a compulsive manner.

What if we don't enrich? Validity of research

In light of the profound influence that environmental enrichment may have on the brain and behavior of laboratory animals, it is important to consider carefully the effects of different housing systems on the external validity of behavioral, physiological, biomedical and neurological studies. For captive housed animals maintained for research purposes, it is important to minimize the effects of environmental stress because accurate research results depend on the animals showing as standard a response as possible. The impact of the housing environment on results from research utilizing laboratory animals is emerging as a valid concern for two main reasons. First, the standard (unenriched) laboratory housing system itself might routinely induce negative mental states such as anxiety that compromise welfare (Wurbel 2001; Garner 2005). Since most research animals spend their entire life in captivity, these animals could be living in a constant state of stress or anxiety. Second, anxiety or fearfulness can substantially influence a range of physiological and behavioral responses which would, in many cases, reduce the validity of the research for which the animals are being housed and, therefore, negate the reason for their being housed in the first place (Wurbel 2001; Sherwin & Olsson 2004; Garner 2005).

The use of animal models in research depends on the assumption that responses of animals from standard conditions are representative of a “normal” biological system and that the study therefore has good external validity. This assumption is not always realized. In weighing

the evidence for the influence of environment on the behavior and biological functioning of animals in captivity, it is clear that environmental enrichment is a key factor in the promotion of animal welfare and the validity of biomedical research conducted with animal subjects.

Constraints on enrichment

Despite the overwhelming evidence of the benefit of environmental enrichment to the welfare of captive animals, enrichment protocols are met with a great deal of resistance by many researchers. Increases in management time and monetary costs associated with the implementation of enrichment protocols often serve as a deterrent to environmental enrichment. Environmental enrichment is constrained by many factors depending on the setting; constraints differ for farm, zoo, and laboratory animals. For instance, enrichment programs for farm animals are constrained by their economic impact on production, whereas enrichment programs for zoo animals are constrained by resource availability, aesthetics, and visitor acceptability (Mench 1998). Ethical concerns arise with the consideration of introducing live prey for captive predators (Newberry 1995; Young 1997). Monetary costs are a concern when considering enrichment for any type of animal and it is, thus, important to determine the enrichments that are most important to the animal's well-being (Dawkins 1990; Mench 1998; Van de Weerd et al. 2003). Environmental enrichment devices are often chosen for their appeal to the investigator, rather than from properties that are salient to the animal. It is always important to consider the functional relevance to the animal when choosing an enrichment device.

Contrafreeloading as enrichment: a simple solution?

In light of the evidence for both domestic and exotic species, environmental enrichment may be a useful tool in mediating the stress levels and performance of abnormal behavior of captive-housed animals. Enrichment may result in a loss or decrease of abnormal behaviors and an increase in behavioral diversity. Enrichment may enable captive animals to cope with challenges in a more normal manner. Opportunities to perform behaviors that are closely linked to the seeking system may provide animals with the stimulation necessary to cope with living in captive environments that differ from the natural environment in which they evolved. If a lack of opportunity to express these behaviors in a constructive manner leads to various negative emotional consequences and abnormal behaviors (Clubb & Mason 2003), provision of contrafreeloading opportunities for captive animals could provide a relatively simple method for improving animal welfare providing that the outcome is not compulsive. Contrafreeloading opportunities can provide many important environmental components simultaneously: choice, opportunities for exploration, cognitive challenge, a means to provide nutrients and an element of control for the captive animal.

The work at hand

In upcoming chapters, I describe a series of experiments on contrafreeloading behavior in captive grizzly bears, chickens and mice. Each study was carefully designed with the animals' natural feeding behaviors in mind, to ensure value in the results in relation to the design of environmental enrichment to improve animal welfare.

Chapter 2 describes two experiments on contrafreeloading behavior in captive grizzly bears (*Ursus arctos horribilis*), designed to advance our understanding of the foraging choices of this species, and to assess information primacy as a possible theoretical foundation for foraging enrichment under captive conditions. Contrafreeloading behavior is investigated in response to concealed food by providing bears with the opportunity extract items from inside ice blocks and cardboard boxes. Implications for environmental enrichment are discussed.

Chapter 3 presents three experiments examining food choice in domestic fowl (*Gallus gallus domesticus*) in relation to the phenomenon of contrafreeloading. In an effort to understand apparent sex differences in cannibalistic tendencies and exploratory behavior in this species, two experiments were conducted in which sex hormones were manipulated. Contrafreeloading behavior, based on level of preference for foraging on small food particles in the presence of larger, more easily consumed, particles (pellets), is compared between treatments. In a third experiment, sex differences are investigated directly, comparing contrafreeloading among individual and paired adult hens and roosters.

In Chapter 4, two experiments are described in which a consumer demand approach was used to assess motivation to contrafreeload in laboratory mice (*Mus musculus*). Information on the strength of motivation to contrafreeload provides insights into whether contrafreeloading is a ‘luxury’ or a behavioral opportunity that mice actively seek.

I conclude in Chapter 5 with a discussion of the major findings and limitations of the studies described within this dissertation, and provide suggestions for future research to help answer questions about the underlying mechanisms behind contrafreeloading.

CHAPTER TWO
CONTRAFREELoADING IN GRIZZLY BEARS: IMPLICATIONS FOR CAPTIVE
FORAGING ENRICHMENT

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ABSTRACT

Contrafreeloading occurs when animals choose resources that require effort to exploit when identical resources are freely available. An apparent contradiction to the basic tenets of optimal foraging theory, contrafreeloading may be a form of exploration where animals compare information about alternative food sources through sampling. To investigate contrafreeloading, we conducted two experiments with captive grizzly bears (*Ursus arctos horribilis*). In experiment 1, bears (n=4) were presented with five foraging choices simultaneously: apples, apple ice-block, salmon, salmon ice-block, and plain ice-block under two levels of food

restriction (ad libitum, 30% of ad libitum). Two measures of contrafreeloading were considered: weight of earned food consumed and time spent working for earned food. More free than earned food was eaten, with only two bears consuming food extracted from ice-blocks, but all bears spent more time manipulating ice-blocks containing salmon or apples than plain ice regardless of level of food restriction. In experiment 2, food-restricted bears (n=6) were presented with three foraging choices simultaneously: apples, apples in box, and empty box. Although they ate more free than earned food, five bears consumed food from boxes and all spent more time manipulating boxes containing apples than empty boxes. These results suggest that, when housed in captivity with access to reliable, easily exploited food sources, bears retain a seeking motivation that is adaptive under natural conditions, where survival is dependent upon finding food in an unpredictable environment. Provision of contrafreeloading opportunities for captive wildlife may enable satisfaction of seeking motivation while avoiding nutritional imbalance.

Keywords: grizzly bears, contrafreeloading, environmental enrichment, exploration, foraging

In considering animal foraging decisions, it is often assumed that animals will act as maximizers, making choices that increase the ratio of nutrient acquisition to effort expended during foraging endeavours. Optimal foraging theory employs the frameworks of adaptation, economics and decision theory to predict the behaviour shown by an “optimal forager,” that is, an animal with perfect ability to maximize reward (MacArthur & Pianka 1966). These early models for the optimal forager made unrealistic assumptions about animal cognitive capacities when considering the ability of animals to estimate patch quality, weigh energetic costs of seeking and

acquiring food and identify energetic gain with near perfect accuracy to produce an optimal foraging strategy (Shettleworth 2001; Andersen et al. 2006). More recent models incorporate measures of memory and decision processing by combining optimal foraging theory with theories of behavioural timing (e.g. 'Scalar Expectancy Theory'--Kacelnik & Brunner 2002), or utilize discrete choice models, to account for what and when animals hunt based on characteristics of prey and predator and non-consummatory 'satisfaction' from prey acquisition (Cooper et al. 2007). These models, nevertheless, make predictions about animal foraging decisions based on maximizing reward. While the behaviour of individual animals inevitably departs to varying extents from that of model optimal foragers, optimal foraging theory is useful for predicting the foraging decisions of animals in variable scenarios (Stephens & Krebs 1986; Alm et al. 2002; Klaassen et al. 2006). Apparent departures from optimality, moreover, often help to identify constraints and deficiencies in models not previously recognized.

One such apparent departure from an optimal foraging strategy is the choice to work for food when identical food is simultaneously available in free form, termed contrafreeloading. Contrafreeloaders choose tasks that require effort over tasks that require negligible effort. Though the phenomenon of contrafreeloading has been documented in several mammalian and avian species in captivity (see Osborne 1977 and Inglis et al. 1997 for reviews), reasons why the animals behave in this manner are poorly understood. An apparent contradiction to the basic tenets of optimal foraging theory, contrafreeloading may be an artefact of captivity. Alternatively, it may represent an adaptive form of exploration where animals seek information about alternative food sources by sampling.

For wild animals facing fluctuations in food abundance in an unstable environment, survival is dependent upon the ability to locate and exploit variable food patches through the performance of appetitive behaviour. This is not a trivial problem, as most foragers will be incompletely informed about the quality of patches prior to exploitation (Klaassen et al. 2006). Survival may be aided by a cognitive capacity to recall and compare the location, nutritional quality and accessibility of alternative food options and make foraging decisions accordingly (Clayton et al. 2005). On arrival at a new food patch, contrafreeloading may thus contribute to immediate decisions about which specific particles to consume in significant amounts within a patch of apparently similar food items. Over a broader scale in both time and space, animals with episodic memory can potentially diminish the risk of starvation in the future by gathering information about resources they do not need immediately but might exploit in the future. In this sense, contrafreeloading has an adaptive value as it is beneficial for animals to invest time and energy in learning about food sites if this knowledge can be exploited during current and future foraging endeavours (Inglis & Ferguson 1986; Dall et al. 2005). Energy spent obtaining information about alternative foraging resources could be recompensed by more efficient intake in the long run.

According to the information primacy hypothesis (Woodworth 1958; Inglis 1983, 2000), the need to reduce environmental uncertainties is a major determinant of behaviour. The incentive to gather information is assumed to be present at all times, but superseded by other motivations when immediate needs arise. A theoretical scaffold for the phenomenon of contrafreeloading, information primacy explains animal foraging decisions based on the interplay between reducing environmental uncertainty and satiating immediate needs. Inglis and

colleagues (1997, 2001) have embraced the information primacy hypothesis in a ‘fuzzy model of contrafreeloading,’ which considers the level of food deprivation, the degree of uncertainty associated with earned food, and the effort required to obtain earned food relative to free food. The model predicts a negative relationship between level of hunger and contrafreeloading, with satiated animals engaging in the most contrafreeloading. Contrafreeloading by satiated animals can be considered a form of intrinsic exploration, whereby animals engage in general exploration rather than appetitive behaviour to meet an immediate need, termed extrinsic exploration (Berlyne 1960). The model also predicts an inverted-u relationship between levels of uncertainty (i.e. novelty, ambiguity or unpredictability) surrounding earned food and contrafreeloading, and a negative relationship between high levels of effort needed to exploit earned food and contrafreeloading.

The limited data supporting the information primacy hypothesis for contrafreeloading have come from domestic rodents and captive and domestic birds (Inglis & Ferguson 1986; Forkman 1991, 1996; Bean et al. 1999; Inglis et al. 2001; Lindqvist et al. 2002). Though there are anecdotal accounts of contrafreeloading by wild animals (e.g. bears continuing to fish for salmon during spawning season when moribund salmon can be easily obtained along the river bank), field studies of contrafreeloading are absent from the literature. Foraging choice is difficult to study in the field because of the wide range of interconnected factors, including competition, reproductive opportunity and predator avoidance, which simultaneously influence a forager. Obstacles are also associated with accurate quantification of food availability and food consumption in natural environments (Gende et al. 2001). Captivity provides an opportunity to test predictions of the information primacy hypothesis under controlled conditions.

Experimental evidence suggests that a motivation to perform appetitive behaviour persists among mammals and birds living in captive environments (Hughes & Duncan 1988; Friend 1989; Jensen & Toates 1993; Haskell et al. 1996; Mench 1998; Sherwin et al. 2004), with neurobiological underpinnings in the seeking circuitry of the brain that gives rise to exploration (Panksepp 1998). Frustration of seeking motivation may lead to its expression in undesirable forms such as stereotyped pacing (Clubb & Mason 2003). Constraints of captive housing have led researchers and caretakers alike to experiment with methods for providing captive animals with the opportunity to express foraging behaviour in otherwise limited enclosures. A strategy often employed is providing animals with the opportunity to work for food through finding, manipulating and extracting food resources. A wide variety of foraging devices that require an animal to work to obtain food is offered to both wild and domestic animals in captivity as a means to diversify foraging behaviour (see Table 1 for a summary). While it is accepted in some circles that allowing animals to work for a proportion of their daily nutritional requirements can be beneficial to their well-being (Markowitz 1982; Carlstead et al. 1991; Lindburg 1998) and thus constitutes a true enrichment of their environment (Newberry 1995), provision of foraging opportunities can be costly and time consuming and the outcome is variable (Table 1), precluding widespread adoption. For wide-ranging species, the success of enhanced foraging opportunities may be more related to their impact on ranging (Clubb & Mason 2007), general exploration or cognitive challenge (Meehan & Mench 2007) than on appetitive components of foraging behaviour, specifically. A more complete understanding of the characteristics of beneficial foraging opportunities and the principles underlying their effectiveness is called for.

In this paper, we explore contrafreeloading behaviour in captive grizzly bears (*Ursus arctos horribilis*) to advance understanding of the foraging choices of this large, wide-ranging, long-lived and cognitively sophisticated omnivore, and to assess information primacy as a possible theoretical foundation for foraging enrichment under captive conditions. We examined contrafreeloading behaviour in response to concealed food, utilizing a species and mode of earning food not previously investigated in contrafreeloading studies. We hypothesized that contrafreeloading enables grizzly bears to gather information about extraction of concealed food resources that could be exploited to a greater extent in the future if more readily accessible food is unavailable. We predicted that bears would spend time attempting to extract concealed foods in the presence of unconcealed (“free”) foods of the same type and that less contrafreeloading would occur under food restricted conditions than ad libitum conditions. Our study involved two experiments conducted in accordance with animal care and use guidelines approved by the Washington State University Institutional Animal Care and Use Committee.

EXPERIMENT 1: SMASH AND GRAB – THE ICE BLOCK CHALLENGE

It has become common practice in the zoo world to provide concealed food inside ice blocks as a form of foraging enrichment for many species. Use of ice blocks as enrichment for captive animals is mentioned in the introduction to the book *Second Nature: Environmental Enrichment for Captive Animals*, where “... scattering an animal’s daily ration around its exhibit, freezing its food into blocks of ice, or hiding it, rather than simply placing it in a bowl...” is recommended (Shepherdson 1998, pg. 1). In an internet search for zoological parks and sanctuaries worldwide that house bears, we found 65 facilities with English web sites that reported using ice blocks

containing food as enrichment specifically for captive bears. Inclusion of ice blocks as appropriate enrichment for bears has spread into popular culture as well, being featured in the virtual zoo of the computer game *Zoo Tycoon*® 2.

Although ice blocks have been reported to add diversity to foraging opportunities (Forthman et al. 1992; Renner & Lussier 2002), ours is the first controlled study, to our knowledge, to provide bears with a simultaneous choice between plain ice, free food and food of the same type concealed in ice, enabling us to measure the relative attractiveness of these elements. The aim of this experiment was to examine contrafreeloading behaviour in grizzly bears by providing them the opportunity to work for food through extracting concealed items from inside ice blocks. We examined one component of the model proposed by Inglis and colleagues (1997, 2001), hunger, by manipulating food restriction levels prior to contrafreeloading trials. We assessed: (1) whether grizzly bears are attracted to ice in general or whether they are specifically attracted to concealed resources, (2) whether grizzly bears contrafreeload, and (3) whether food restriction level affects the level of contrafreeloading in grizzly bears.

Methods

Bear Facility

We conducted contrafreeloading trials with captive grizzly bears housed at the Washington State University Bear Research, Education, and Conservation Facility in Pullman, WA. During most of the year, bears in this facility are provided free access to a 32 m² indoor-outdoor pen combination and a 0.81 ha outdoor semi-natural enclosure. Each indoor pen (3.3 x 3.3 m) is

visually isolated and temperature controlled to aid bears in seasonal thermoregulation. The outdoor pens and semi-natural enclosure are open to the elements, so conditions in these areas fluctuate with the natural weather patterns of the area. Each outdoor pen is equipped with a hanging tire and wooden log. Bears are given access to the semi-natural enclosure between 0700 h and 1500 h and spend the remainder of the time in their indoor-outdoor pen combination. They are generally housed in pairs, and socialize with additional bears through the outdoor pen fencing and directly when released together in the semi-natural enclosure. They are typically fed one large meal at 0700 h and given a small food reward at 1500 h to draw them in from the semi-natural enclosure. Water is provided ad libitum through water licks and a large outdoor water tub. The bears hibernate from late October through early April and are active for the remainder of the year.

Ice Blocks

Ice blocks were constructed by filling a 9.5 L round plastic bucket (23.9 cm high; 25.4 cm diameter) with water and freezing at -2°C for 48 h. To conceal food items in the centre of ice blocks, the ice blocks were constructed in two stages: 1) buckets containing 4.7 L of water plus the food items floating at the surface, were placed in a freezer for 24 h; 2) an additional 4.7 L of water was added and the contents of the buckets were frozen for a further 24 h. Blocks free of food were constructed in the same manner to assure uniformity in the freezing patterns of the ice.

Both salmon and apples were frozen in ice blocks. Intact salmon were cut dorso-ventrally into segments approximating 500 g, and one segment was frozen within each salmon ice block. Approximately 500 g of apples were frozen into apple ice blocks. Whole apples were punctured

to allow escape of juices into the water during freezing to mimic the escape of juices from salmon segments.

Experimental Design

Experiment 1 was conducted with four wild born adult grizzly bears, Bo and Irving (18-year-old brothers, weighing approximately 360 kg) and June and Patches (unrelated 17-year-old females, weighing approximately 180 kg). For the purpose of the experiment, we housed each bear temporarily in an indoor-outdoor pen, with the indoor portion of the pen serving as the test arena. Testing indoors allowed for visual isolation during the experimental trials to prevent social learning of foraging preferences and tactics. It also provided uniformity in temperature and light intensity in the test arenas between individuals. Bears were temporarily denied access to the semi-natural enclosure to control feed intake by preventing foraging on clover and grasses. The experiment was conducted from late August through early October, just prior to hibernation, when the bears are physiologically adapted to putting on fat stores (Hilderbrand et al. 1999).

Bears participated in six 1-h foraging choice trials (one trial per day) and were in the study for a total of 11 days. Each bear was subjected to two experimental treatments: (1) food restriction (30% of ad libitum, typical for non-lactating adult bears in this facility) and (2) ad libitum food. Foraging choice trials under the food restriction condition were conducted on the first three days. After a five day transition period during which bears were fed ad libitum and allowed to reach satiation, three days of ad libitum foraging choice trials were conducted.

During each trial, bears were presented simultaneously with five foraging choices placed in separate locations on the pen floor: (1) free apples (a pile of fresh Fuji and Macintosh apples), (2) free salmon (a pile of frozen Pacific salmon), (3) a plain ice block, (4) earned apples (a mixture of Fuji and Macintosh apples frozen inside an ice block) and (5) earned salmon (Pacific salmon frozen inside an ice block). Plain ice blocks were provided as a control for attraction to ice. The placement of each foraging option within the test arena during successive trials was randomized through a Latin Square design to control for any location bias.

Trials were conducted at 0700 h each morning after the pens had been cleaned and a known quantity of each foraging option had been placed in the test arena. Two bears (one male and one female) were tested consecutively each morning in a counterbalanced order. The duration of the trials was limited to 1 h to minimize the amount of ice that melted, since melting would result in the earned food becoming transformed into free food. At the end of the trial, the amount of each foraging choice remaining was weighed back.

On food restriction days, we kept bears on maintenance level food restriction (30% of ad libitum) by feeding them their daily allowance of salmon and apples during the foraging choice trial, with any remaining food being returned at the end of the trial. The amount of food provided was calculated based on body weight (approximately, 0.035 and 0.045 kg/kg body weight, salmon and apples, respectively) to ensure that each bear was receiving appropriate nutrient levels to maintain a healthy body weight. Following trials on ad libitum days, bears were provided with continued free access to food by adding salmon and apples as needed throughout the day.

Data Collection

The weight of each foraging choice was measured before and after each trial to enable calculation of the amount of each type of food consumed. When ice blocks were broken by the bears, the pieces were collected for weigh back. During each trial, a Psion Workabout® handheld computer (Psion PLC, London, UK) equipped with The Observer® Version 4.0 (Noldus Information Technology, Wageningen, The Netherlands) was used to record each focal animal's behaviour continuously for 1 h by direct observation through an observation window. All transitions between non-contact investigation, manipulation of each foraging choice and other behaviour (Table 2) were recorded, from which the total time spent in each behaviour category per hour was calculated. All data were collected by the same observer.

Statistical Analysis

Data for non-contact investigation, manipulation and consumption were analyzed separately. We used a mixed linear model (Proc Mixed) of the SAS Institute (1999), with foraging choice as a repeated measure, to assess the effects of food restriction, sex, trial (1-6) and their interactions on the bears' behaviour toward the foraging options. Bear within sex and bear by trial within sex were random terms in our model. Our subject effect was bear by trial and we included a contrast statement (trial -1 -1 -1 1 1 1) to assess the effects of food restriction treatment. Because the residuals were not normally distributed, we applied the mixed linear model to $\log(Y+1)$ transformed data to meet the assumptions for use of parametric statistics. Comparisons between foraging options were made based on differences in least-squares means, with p-values adjusted

for multiple comparisons using the Tukey option. Significance level for all statistical computations was set at $\alpha=0.05$.

Results

Bears approached and began to explore the foraging choices immediately upon admittance to the test arena. During initial non-contact investigation, bears typically spent 2-3 s over each foraging choice, sniffing and inhaling deeply before moving on to the next item. A manipulation phase reliably followed whereby bears would physically interact with the items. Bears began by pawing at ice blocks and then pushing them along the floor of the pen with their noses while continuing olfactory investigation. Initial manipulation of the free food items generally involved mouthing and licking. Almost invariably, after a period of manipulating foraging choices, the bears consumed some portion of free food before returning to the ice blocks, and then alternated between “free food” and “earned food” choices.

There was a difference in the amount of time spent in non-contact investigation between the five foraging items (Mixed linear model: $F_{4,68}=5.43$, $P=0.0007$) with bears spending more time investigating free than earned apples and salmon (Tukey adjusted t test: $t_{68} \geq 2.04$, $P<0.05$; Figure 1). There were no differences in non-contact investigation due to food restriction (Mixed linear model: $F_{1,15}=1.71$, $P=0.21$), sex ($F_{1,2}=0.53$, $P=0.54$), trial ($F_{5,15}=0.74$, $P=0.60$) or their interactions ($P \geq 0.092$).

There were significant differences in time spent manipulating the five foraging options (Mixed linear model: $F_{4,68}=36.09$, $P<0.0001$; Figure 2). Bears spent significantly more time

manipulating free apples and salmon than ice blocks containing these foods (Tukey adjusted t test: $t_{68} \geq 3.4$, $P \leq 0.010$; Figure 2). A closer look at the bears' interactions with the ice blocks reveals that bears spent more time manipulating ice blocks containing food than plain ice blocks (Tukey adjusted t test: $t_{68} \geq 3.4$, $P \leq 0.010$; Figure 2), indicating that they attempted to exploit food within the ice blocks even though they were not always successful. We detected no significant effects of food restriction (Mixed linear model: $F_{1,15} = 0.91$, $P = .36$), sex ($F_{1,2} = 0.37$, $P = 0.61$), trial ($F_{5,15} = 1.26$, $P = 0.33$) or their interactions ($P \geq 0.051$) on time spent manipulating foraging choices.

Two bears (Bo and June) were successful in accessing food extracted from ice blocks, all of which was consumed. Bo broke ice blocks open by picking them up and tossing them against the wall of the test arena (Figure 3) while June pawed at and chewed ice blocks until the food within was exposed. We found no effects of sex (Mixed linear model: $F_{1,2} = 1.19$, $P = 0.39$), trial ($F_{5,15} = 2.74$, $P = 0.060$) or their interactions ($P \geq 0.133$) on amount of food consumed. There were differences in consumption of the four food options (Mixed linear model: $F_{3,51} = 89.45$, $P < 0.0001$). Tukey-adjusted t tests showed that bears consumed more free (apples + salmon, mean \pm SE, 13.17 ± 1.06 kg) than earned (apple ice + salmon ice, 0.14 ± 0.04 kg) food ($t_{17} = 12.80$, $P < 0.0001$) and ate more free apples than free salmon ($t_{51} = 3.22$, $P = 0.012$) during the 1-hour test sessions (Figure 4). There were differences in consumption due to food restriction (Mixed linear model: $F_{1,15} = 6.56$, $P = 0.022$). The bears ate smaller quantities of free apples and free salmon during the 1-h trials when fed ad libitum than when food restricted (Figure 4).

EXPERIMENT 2: RIP AND SHRED – DOES LESS EFFORT PROPEL CHOICE TO WORK?

In experiment 1, only two bears were successful in extracting and consuming concealed food from the ice blocks. The aim of experiment 2 was to create a scenario that might provide more information about the propensity of bears to contrafreeload by reducing the level of effort required to extract concealed food. We thus replaced ice blocks with cardboard boxes in this experiment. Cardboard boxes are often employed as enrichment devices for captive wild and domestic animals due to their malleable, destructible and non-toxic properties (Table 1; Van de Weerd et al. 2003). We assessed: (1) whether bears are attracted to cardboard boxes in general or whether they are attracted to concealed resources and (2) whether bears contrafreeload when they are food restricted and the effort required for obtaining earned food is low.

Methods

Subjects

Grizzly bear subjects in this experiment were two sub-adult brothers (John and Frank, 2 years old, approximately 120 kg) and four unrelated adult females (June, Patches, Annie and Star, 17-18 years old, approximately 180 kg), all wild born and housed in an identical manner to the bears in experiment 1.

Experimental Design

Given that the results of experiment 1 indicated no effect of food restriction on the level of interaction with each foraging item, all bears in this experiment were kept on maintenance level

food restriction (approximately 30% of ad libitum) and were fed their daily ration (a mixture of fresh apples of Fuji and Macintosh varieties, approximately 0.08 kg/kg body weight) in one large meal at 0700 h. The experiment was conducted from late April through May, just after the bears came out of hibernation.

Each bear participated in three 1-h trials (one trial per day) and was in the experiment for a total of three consecutive days, with two bears being tested consecutively each morning following the same procedure as in Experiment 1. During each trial, bears were presented simultaneously with three foraging choices: (1) free apples, (2) earned apples and (3) cardboard. Free apples (approximately 0.04 kg/kg body weight) were presented in a pile on the floor of the test arena and earned food took the form of apples (approximately 0.04 kg/kg body weight) enclosed in a brown cardboard box (45.7 cm long x 45.7 cm wide x 61.0 cm high). A closed empty cardboard box of the same size and construction was provided as a control for attraction to cardboard.

Data Collection and Analysis

During each trial, the bears' interactions with each foraging choice were recorded continuously for 1 h as in experiment 1. The amount of free food and earned food presented in boxes was weighed before and after each trial, and the amount of food consumed from each source was calculated. Statistical analyses were conducted as described in experiment 1.

Results

As in experiment 1, bears were quick to approach and interact with each foraging option. Bears sniffed at the free apples and at each box before manipulation and apple consumption. Time spent in non-contact investigation did not differ between the free apples (mean \pm SE, 12.9 ± 2.3 s), the earned apples (13.7 ± 2.3 s), and the empty box (14.0 ± 3.3 s) (Mixed linear model: $F_{2, 28}=0.60$, $P=0.56$). We found no effects of sex (Mixed linear model: $F_{1,4}=5.12$, $P=0.086$) or trial ($F_{2,10}=1.24$, $P=0.33$) on non-contact investigation.

As was expected, opening boxes proved to be a relatively simple task. Bears employed multiple tactics for extracting concealed food from within the boxes, ranging from gently opening the top of the box with the nose to crushing the box and tearing it open to extract the apples. There were significant differences in time spent manipulating the three foraging options (Mixed linear model: $F_{2, 28}=14.24$, $P<0.0001$; Figure 5). Tukey-adjusted *t* tests showed that bears spent a similar amount of time manipulating free apples and boxes of apples ($t_{28}=1.26$, $P=0.43$) whereas they spent less time manipulating empty boxes than boxes of apples ($t_{28}=3.86$, $P=0.0017$; Figure 5). We found no effect of sex (Mixed linear model: $F_{1,4}=0.55$, $P=0.50$), trial ($F_{2,10}=1.04$, $P=0.39$) or the interaction between trial and foraging choice ($F_{4,28}=0.90$, $P=0.48$) on time spent manipulating the three foraging options. There was a significant interaction between sex and time spent manipulating the different foraging choices ($F_{2,28}=11.50$, $P=0.0002$), with the two sub-adult males manipulating boxes with apples (mean \pm SE, 729.5 ± 92.4 s) more than free apples (321.7 ± 64.4 s) and the four adult females spending more time manipulating free apples (1271.4 ± 47.7 s) than boxes with apples (331.6 ± 55.4 s; Tukey adjusted *t* test: $t_{28}=4.63$, $P=0.001$).

Five bears were successful in extracting and consuming food concealed inside boxes (2 males and 3 females). Though they were successful in accessing the concealed food, none of the bears consumed the full quantity of apples offered in the box. The three females consistently left uneaten apples inside the opened box, except on one occasion where one female tipped over the box and dumped the apples onto the floor. During the first two days of testing, the two males also left some portion of uneaten apples inside the box, but on the third day of testing both males shredded their boxes spilling uneaten apples to the floor. Due to adequate spacing of the foraging options across the floor of the home pen, apples spilled from the boxes were only mixed with free apples on two occasions. In both cases, the number of apples that rolled into the 'free' pile was noted and the difference was accounted for during weigh-back at the end of the test session.

Whereas bears in experiment 1 generally consumed some portion of free food before attempting to extract food from ice blocks, bears in this experiment frequently consumed earned apples before free apples. There were no differences in food consumption due to sex ($F_{1,4}=1.30$, $P=0.32$) or trial ($F_{2,10}=0.34$, $P=0.72$). There was a difference in consumption of the two food options ($F_{1,14}=5.57$, $P=0.033$). On average, the six bears consumed more free apples than earned apples during the 1-h observation sessions (Tukey adjusted t test: $t_{14} = 2.36$, $P=0.033$). There was no interaction between trial and food choice ($F_{2,14}=0.65$, $P=0.54$), but a significant interaction between sex and food choice ($F_{1,14}=8.28$, $P=0.012$). The two sub-adult males tended to eat more apples from boxes (mean \pm SE, 3.2 ± 0.5 kg) than free apples (2.4 ± 0.6 kg) whereas the four adult females ate more free (6.8 ± 0.4 kg) than boxed apples (1.1 ± 0.3 , Tukey adjusted t test: $t_{14} \geq 2.38$, $P \leq 0.033$).

DISCUSSION

What constitutes “contrafreeloading”?

Under choice paradigms where an effortful or relatively effortless response leads to the same reinforcer, it has been shown that animals will respond for resources in the presence of freely available identical resources (contrafreeloading), and sometimes prefer to obtain resources via the more effortful response (Taylor 1972; Osborne 1977; Inglis et al. 1997; Colman 2006). The literature on contrafreeloading often involves working for food. In this scenario, intake of earned food in the presence of free food is usually used as the criterion for contrafreeloading. Some authors have gone further, considering that contrafreeloading has occurred only if the proportion of earned food consumed exceeds a specific level, varying across studies from 10% (Kopp et al. 1976) to 50% (Osborne 1977) or a majority (>50%, Inglis et al. 1997, 2001; Lindqvist et al. 2002, 2006) of total food consumed. These variations in defining the phenomenon of contrafreeloading appear arbitrary and confusing.

Defining contrafreeloading based on some proportion of earned food consumed excludes studies which explore the phenomenon using non-nutritive resources (e.g. working for marbles (children--Singh 1970), mirrors (Siamese fighting fish *Betta splendens*--Baenninger & Mattleman 1973), or coins (adult humans--Tarte 1981)), and sets limitations on exploring the robustness of the phenomenon across experimental paradigms incorporating a whole suite of resources. Animals have been observed to work for consumable resources that they choose not to consume, suggesting that effort in resource acquisition does not directly parallel resource-

consuming behaviour. Wild rats will work for contaminated food that they associate with sickness and subsequently reject (Inglis & Shepherd 1994), birds respond for earned food that they do not eat (Neuringer 1969), and rats work for water that they do not drink (Amato et al. 2006), even when the same resources are freely available. Some authors have, thus, considered that any work or effort expended to acquire access to a resource in the presence of an easier alternative for obtaining the same resource constitutes contrafreeloading, quantifying the level of contrafreeloading using measures such as the distance travelled in a maze (Havelka 1956), number of bar presses expended (Knutson & Carlson 1973; Inglis & Shepherd 1994) and number of swims through a hoop (Baenninger & Mattleman 1973) to access food in the presence of the same food accessible without performing these activities. Given that optimal foraging models predict an absolute preference for consuming easy-to-obtain food over food of the same type requiring effort to exploit, any deviation from this prediction must be explained (Stephens & Krebs 1986). We propose, therefore, that the concept of contrafreeloading should not be limited to situations in which a large proportion of food is consumed in earned form. From this perspective, it is useful to include as contrafreeloading any level of effort devoted to working for a resource in the presence of the same resource in an easily exploited form.

Contrafreeloading: appetitive or consummatory behaviour?

In this study, we have used two broad measures of contrafreeloading behaviour, the first dealing with consumption (weight of earned food consumed) and the second dealing with work invested in earning a food resource (time spent manipulating earned food) in the presence of the same food in a more easily exploited form. By the latter measure, all of the grizzly bears engaged in contrafreeloading in our experiments. The bears spent more time manipulating devices that

contained concealed food than devices without food, showing that they were motivated to explore concealed resources and were not solely attracted to plain ice or empty cardboard boxes. The observation that bears did not always immediately consume the extracted food suggests that consumption is not an exclusive motivating factor, or the sole benefit, of appetitive behaviour.

Contrafreeloading behaviour may reflect an inherent predisposition for animals to seek out information about the quality and accessibility of different resources (Inglis 2000). Knowledge gained through contrafreeloading at times of resource abundance can then be applied in the future when resources may be more sparse. Whereas this behaviour would have adaptive benefits in the wild, it could seem “unnecessary” in captivity when animals are provided with food ad libitum. Yet captive and domesticated animals retain a strong internally driven motivation, rooted in the extended lateral hypothalamic corridor of the mammalian brain (Panksepp 1998; Inglis 2000; Everitt et al. 2001; Spruijt et al. 2001), to explore and learn about environmental contingencies. A lack of opportunity to express this behaviour in a constructive manner may lead to various negative emotional consequences and abnormal behaviours (Clubb & Mason 2003).

Both food and information act as incentives determining an animal’s foraging choices. The ‘fuzzy model’ (Inglis et al. 1997, 2001) predicts that contrafreeloading should arise only as physiological needs decrease. We investigated the effects of ‘physiological need’ on contrafreeloading by testing bears under two levels of food restriction. Despite variation in satiety level, all bears sought opportunities to investigate and manipulate concealed food sources when the same food was freely available. Under our experimental protocol, physiological need

had little effect on a bear's choice to manipulate concealed food items. It is possible that food restriction to 30% of ad libitum did not produce a fervent sense of food deprivation in the bears. Considering, however, that the first experiment was conducted in the weeks immediately preceding hibernation, when bears experience an elevated physiological motivation to put on fat stores (Hilderbrand et al. 1999; Rode et al. 2001), food restriction to 30% of ad libitum consumption should have elicited intense hunger levels. It is unlikely that our attempt to satiate the ad libitum-fed bears failed to produce a period of very low hunger levels given that the bears were allowed to feed freely for five days prior to testing under this condition. During this time the amount of food bears consumed each day decreased and their latency to approach free food increased, a pattern consistent with a decreasing hunger level (Lawrence et al. 1988; Vickery & Mason 2005). Our low sample size may not have allowed for a detection of food restriction effects. The alternative is that motivation for contrafreeloading by grizzly bears is less affected by physiological needs than predicted, a finding that would correspond with studies of carnivores where that the decision whether or not to hunt is independent of hunger level (e.g. cheetahs, Cooper et al. 2007).

When housed in captivity with access to reliable, easily exploited food sources, bears may retain a seeking motivation that is adaptive under natural conditions, where survival is dependent upon finding food in an unpredictable environment. Panksepp (1998 pg. 145) describes a “foraging/exploration/investigation/curiosity/interest/expectancy/SEEKING system” that leads animals to explore everything in their environments from “nuts to knowledge.” Appetitive behaviours appear to be regulated by this ‘seeking’ system, while consummatory behaviours are regulated by a separate ‘pleasure’ system (Panksepp 1998). At least in humans,

stimulation of the seeking system is accompanied by an intense feeling of interest about one's surroundings (Heath 1963), as opposed to the sense of pleasure associated with consumption. In this respect, the seeking system may motivate animals to perform appetitive behaviour, regardless of whether the animal is experiencing a physiological need for an ultimate goal to be satisfied (Panksepp 1998; Jones & Pillay 2004). Studies of neuronal activity in the seeking circuitry of the brain indicate that this system is distinctly reactive to stimuli that predict rewards, rather than to rewards themselves. For example, neurons within the trajectory of the seeking system are aroused when animals are searching for food and shut down promptly when food is found and feeding begins (Hamburg 1971; Aou et al. 1991; Panksepp 1998). Upon entrance into the test arena, bears may have been propelled by the seeking system to explore and gather information about the foraging items (continuous) until encountering a need-relevant resource, triggering anticipation for reward and shifting the bear into a consummatory (episodic) mode (Panksepp 1998). Our observation of bears alternating between manipulating concealed food resources and consuming free food is consistent with switching back and forth between 'seeking' and consummatory systems.

Is there such a thing as too much work? 'Learned industriousness' and contrafreeloading

The 'fuzzy model' of contrafreeloading (Inglis et al. 1997, 2001) predicts that an increase in the effort required to obtain earned food items will lead to a reduction in contrafreeloading behaviour. In experiment 1, we aimed to design a device that would require an intermediate level of work for the bears to extract concealed food. It was a challenge to develop a task that would constitute effort for animals of the size and strength of grizzly bears (known for their destructive capabilities when it comes to cars and campsites). We opted to use ice blocks to conceal earned

food items with the expectation that, given their popular use as enrichment devices in zoos, breaking ice blocks would be a feasible, but challenging, task for grizzly bears. The task proved to be quite difficult within the time frame of our observations (1 h, to minimize melting of the ice) resulting in limited success by bears in their attempts to extract earned food items. Observation of bears for longer intervals may be necessary to witness extraction of additional food from within ice blocks (Renner & Lussier 2002). In experiment 2 we choose to conceal food inside cardboard boxes to provide bears with a task that required less effort than breaking ice blocks for the extraction of resources. With this reduced effort requirement, more bears were successful in extracting and consuming earned food items, consistent with the predictions of the ‘fuzzy model’ (Inglis et al. 1997, 2001).

Taken together, our results from the ice-block and box experiments point out a limitation of optimal foraging hypotheses, indicating that in some scenarios animals choose more costly options over energy maximizing options. It may be incorrect to assume that animals find increased effort aversive. A counterpart to the ‘law of least effort’, from which optimal foraging theories are derived, the theory of ‘learned industriousness’ is built upon the potentially rewarding properties of effort. Eisenberger (1992) posed that if individuals receive a reward for expending a large amount of effort on an activity (e.g. consumption of food after working to obtain the food), the sensation of high effort becomes associated with reward, thereby increasing an individual’s readiness to expend high effort on subsequent tasks. In choice situations, individuals who have acquired this ‘learned industriousness’ are predicted to show increasing preference for high-effort tasks that produce a larger magnitude of reinforcement (due to positive association with high effort) relative to low-effort tasks that yield a smaller magnitude of

reinforcement (due to lack of positive association with low effort). In this sense, the aversiveness of work in a broad range of behaviours may be altered by learning (Eisenberger 1992; Ingis & Shepherd 1994). The notion of 'learned industrious' may be a reflection of increased anticipation for a reward. Under some experimental conditions animals appear to be natural optimists when it comes to reward expectancies. For example, rats working for food on a fixed interval schedule in an operant chamber will gradually increase their response rate (lever presses) as the time for reward approaches (Panksepp 1998). This self-imposed intensification of work before an expected reward may represent an increased level of excitement or anticipation for the impending result. In this sense, work is not aversive, but rather exciting.

Contrafreeloading: does age matter?

To our knowledge, previous studies have not examined age in relation to the performance of contrafreeloading behaviour but several authors have examined effects of age on exploration and interaction with enrichment items and the results are wide ranging. For the octopus, age seems to have little effect on exploration, with adults and sub-adults demonstrating similar levels of exploration and play in relation to novel objects (Kuba et al. 2006). Adult pandas, on the other hand, demonstrate preference for enrichment items that offer food rewards over enrichment items that provide no food rewards, whereas sub-adults will interact with these items equally (Swaigood et al. 2001). Similar age differences have been observed in chimpanzees, where mirror use decreases after multiple exposures in adults, but increases with multiple exposures in young animals (Lambeth & Bloomsmith 1992). Among animals that disperse from their parents, juveniles are often more likely to explore new food sources (Cambefort 1981) and engage in more risky behavior (Spear 2000) than adults. For example, adolescent mice appear hyperactive

in novel environments, demonstrating more exploratory behavior (Darmani et al. 1996) and higher levels of novelty seeking than their adult counterparts (Adriani et al. 1998).

In our study, male sub-adult bears manipulated and tended to consume earned food items more than free food items. This was in contrast to adult bears who manipulated and consumed free food items more than earned food items. Our findings suggest that younger animals may be more motivated to perform contrafreeloading behaviour than adult animals. In terms of information gain, this finding is logical as younger animals will have more to learn about their environment than older animals. For sub-adult animals that are dispersing from their natal range, potential new food sources must be located and experience in locating and accessing unfamiliar food items could contribute to future foraging success. For example, in howler monkeys it has been estimated that emigrating adolescents encounter less than 40% of the plant species of their natal habitat (Crocket 1987), making it essential for these animals to have the skills necessary for identifying alternative food sources. Contrafreeloading may reflect an attraction towards risk, or “temptation to gamble” (Adriani & Laviola 2006) because animals choose resources that are uncertain when more reliable resources are available. Increased contrafreeloading by the sub-adult males in our study may, thus, be a reflection of increased willingness to take risks, and having more to learn from such risks, than the adult bears.

Contrafreeloading: implications for captive feeding regimens

The animals in our study demonstrated particular attraction to concealed food items that could be extracted from malleable objects rather than similar objects lacking food. This finding provides experimental evidence to support the use of foraging enrichment over the provision of “toys” that

lack functional relevance to the animals (Newberry 1995). When animals are unable to perform both appetitive and consummatory components of complex natural behaviours, their welfare may be compromised (Hughes & Duncan 1988; Spruijt et al. 2001; Clubb & Mason 2007). Provision of contrafreeloading opportunities for captive wildlife may have advantages over provision of novel foods that are different from the regular, nutritionally balanced “chow” by enabling satisfaction of seeking motivation while avoiding nutritional imbalance.

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Table 1. Survey of effects of foraging enrichment techniques incorporating “working” for food on commonly-reported dependent variables, across a range of species held in captivity¹

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Sound activated “Fish Catapult”	<i>Ursus maritimus</i>	Polar bear	+	-	-	+	NM	Markowitz (1982)
Food inside ice blocks	Various	Primates	+	V	-	+	NM	Chamove et al. (1982); Survey by Howell & Fritz (1999)*; Reviewed by Honess & Marin (2006)*
	<i>Ursus arctos middendorffii</i>	Kodiak bear	NR	-	NM	+	NM	Forthman et al. (1992)
	<i>Ursus maritimus</i>	Polar bear	NR	V	NM	+	NM	Forthman et al. (1992)
	<i>Ailuropoda melanoleuca</i>	Giant panda	+	V	NM	+	NM	Swaigood et al. (2001; 2005)

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Fresh browse	<i>Selenarctos thibetanus</i>	Asiatic black bear	NR	V	NM	+	NM	Forthman et al. (1992)
	<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	+	NS	-	+	NM	Rooney & Sleeman (1998)
	<i>Ailuropoda melanoleuca</i>	Giant panda	+	V	NM	+	NM	Swaigood et al. (2001; 2005)
Food inside cardboard boxes	<i>Hystrix cristata</i>	African crested porcupines	+	NM	NM	+	HM	Bartos (1998)*
	<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	+	NS	-	+	NM	Rooney & Sleeman (1998)
	<i>Pan troglodytes</i>	Chimpanzee	+	NM	NM	+	NM	Survey by Howell & Fritz (1999)*; Reviewed by Honess & Marin (2006)*
Food inside wobbling bottle caps	<i>Coturnix coturnix japonica</i>	Japanese quail	+	-	NM	+	NM	Miller & Mench (2005)
Bat grenade	Various species	Bats	+	NM	NM	+	NM	Chag (1996)*

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Filled logs	Melursus urinus	Sloth	-	-	NM	NS	+	Carlstead et al. (1991)
	Ursus americanus	Black bear	NS	NS	NM	NS	NM	Carlstead et al. (1991)
Foraging boards— Astroturf, fleece, etc.	Various species	Primates	+	V	V	+	NM	Fekete et al. (2000); Reviewed by Honess & Marin (2006)*
	Coturnix coturnix japonica	Japanese quail	+	-	NM	+	NM	Miller & Mench (2005)
Puzzle feeder	Various species	Octopus	+	-	NM	+	+	Wood & Wood (1999)*; Rehling (2000)
	Ailuropoda melanoleuca	Giant panda	+	V	NM	+	NM	Swaigood et al. (2001; 2005)
	Papio hamadryas hamadryas	Hamadryas baboon	+	NM	V	+	NM	Jones & Pillay (2004)

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Puzzle Feeder	Various species	Primates	+	-	V	+	+	Reviewed by Honess & Marin (2006)*
Dispersing food throughout enclosure	<i>Ursus americanus</i>	Black bear	+	-	NM	NS	NM	Carlstead et al. (1991)
	<i>Felis Bengalensis</i>	Leopard cat	+	-	NM	+	NM	Shepherdson et al. (1993)
	<i>Elephas maximus</i>	Asian Elephant	NS	NM	NM	NS	NM	Weidenmayer (1998)
	<i>Tremarctos ornatus</i>	Spectacled bear	+	NS	NM	+	NM	Fischbacher & Schmid (1999)
	Various	Octopus	+	-	NM	+	NM	Wood & Wood (1999)*
	<i>Ursus arctos</i>	Brown bear	+	-	NM	+	NM	Morimura & Ueno (1999)
	Various	Primates	+	V	V	+	NM	Reviewed by Honess & Marin (2006)*

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Dispersing food throughout enclosure	<i>Vicugna vicugna</i>	Vicugna	+	+	NM	+	NM	Parker et al. (2006)
Mechanical feeding tree	<i>Ursus americanus</i>	Black bear	+	NS	NM	NS	NM	Carlstead et al. (1991)
Food in basket, cage or net	Various	Primates	+	NM	NM	+	NM	Survey by Howell & Fritz (1999)*; Reviewed by Honess & Marin (2006)*
	<i>Equus caballus</i>	Domestic Horse	+	-	NM	NS	MN	Goodwin et al. (2002); Thorne et al. (2005)
	<i>Amazona amazonica</i>	Oranged-winged amazon parrot	+	-	NM	NM	NM	Meehan et al. (2003)

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Food in cage, basket or net	<i>Eulemur macaco</i> <i>macaco</i> ; <i>Lemur catta</i>	Black lemur; Ringtail Lemur	NS	-	NM	+	NM	Maloney et al. (2006)
Food inside bag – paper or cloth	<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	+	NS	-	+	NM	Rooney & Sleeman (1998)
	<i>Ailuropoda melanoleuca</i>	Giant panda	+	V	NM	+	NM	Swaigood et al. (2001; 2005)
	<i>Amazona Amazonica</i>	Oranged-winged amazon parrot	+	-	NM	NM	NM	Meehan et al. (2003)
Mixing food in substrate (ie.g. woodchips, gravel or sand)	<i>Macaca arctoides</i>	Stump-tailed macaque	+	-	-	+	NM	Chamove et al. (1982); Wolfensohn & Honess (2005)
	<i>Odobenus rosmarus divergens</i>	Pacific walrus	+	-	NM	+	NM	Kastelein & Wiepkema (1989)

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Mixing food in substrate (ie.g. woodchips, gravel or sand)	<i>Cercocebus torquatus</i> <i>torquatus</i>	Red-capped mangabey	+	-	V	+	NM	Blois-Heulin & Jubin (2004)
	<i>Papio hamadryas</i> <i>hamadryas</i>	Hamadryas baboon	+	NM	-	+	NM	Jones & Pillay (2004)
	<i>Coturnix coturnix japonica</i>	Japanese quail	+	-	NM	+	NM	Miller & Mench (2005)
	Various	Primates	+	-	V	+	NM	Reviewed by Honess & Marin (2006)*
	<i>Eulemur macaco macaco; Lemur catta</i>	Black lemur; Ringtail Lemur	NS	-	NM	+	NM	Maloney et al. (2006)
Edinburgh Foodball (or variant)	<i>Sus scrofa</i>	Domestic swine	+	NM	NM	+	NM	Young et al. (1994)

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Edinburgh Football (or variant)	<i>Equus caballus</i>	Domestic horse	+	-	NM	+	NM	Malpass & Weigler (1994); Winskill et al. (1996); Henderson & Waran (2001)
Encapsulate d foods and tools for opening them	<i>Anodorhynchus hyacinthinus</i>	Hyacinth macaw	+	NM	NM	NM	+	Borsari & Otteni (2005)
Termite 'fishing' mound	<i>Pan troglodytes</i>	Chimpanzee	+	-	NM	+	+	Maki et al. (1989); Survey by Howell & Fritz (1999)*
Carcass feeding	Various	Felids	V	-	V	V	+	Reviewed by Young (1997)* & Houts (1999)*; McPhee (2002)
Live prey	<i>Suricata suricata</i>	Meerkat	+	NS	NM	+	NM	Shepherson et al. (1989)

Method	Species	Common Name	Outcome					References
			Foraging behaviour	Abnormal behaviour	Agonistic behaviour	Time spent active	Foraging skills	
Live prey	<i>Felis viverrina</i>	Fishing cat	+	NS	NM	+	NM	Shepherdson et al. (1993)
	<i>Enteroctopus dofleini</i>	Giant pacific octopus	+	NM	NM	+	+	Reviewed by Anderson & Wood (2001)*
	<i>Salmo salar</i> L. parr	Atlantic salmon	+	NM	NM	NM	+	Brown et al. (2003)
	Various	Primates	+	-	V	+	NM	Reviewed by Honess & Marin (2006)*
	<i>Eulemur macaco macaco</i> ; <i>Lemur catta</i>	Black lemur; Ringtail Lemur	NS	-	NM	+	NM	Maloney et al. (2006)

¹Databases searched: Science Direct, Biosis, Web of Science, Scirus, AGRICOLA. Keywords: contrafreeloading, foraging enrichment, environmental enrichment, behavioural enrichment, working for food, feeding, foraging behaviour, captive animals. Outcomes: + increase, - decrease, V variable, NS not significant, NR not reported, NM not measured. * Papers reviewing effects without presenting statistics.

Table 2. Ethogram

Behaviour category	Description	Definitions of behavioural elements occurring within each category
Non-contact investigation	Bear orients nose within one head's length of foraging item and visually inspects, sniffs or inhales deeply	Visual Inspection: bear's gaze directed at foraging item Sniff: movement of nostrils, short breaths inhaled through nose
Manipulation	Bear physically interacts with foraging item. Tactile exploration of foraging item including, but not limited to: pawing or swatting, picking up or tossing, licking or chewing and consuming food item	Paw: bear pushes or rolls foraging item on the ground using its forepaw(s) Swat: quick and direct movement of paw towards foraging item Pick up: bear lifts food item from floor and holds or rotates object in forepaws and/or hind-paws Toss: bear releases food item from grip, launching towards pen wall or floor Chew: bear's jaw moves vertically crushing substance
Null	Behaviour not involving interaction with a foraging item, including, but not limited to: resting, urinating, defecating, looking out or sniffing through the pen door, and vocalizing	Variable

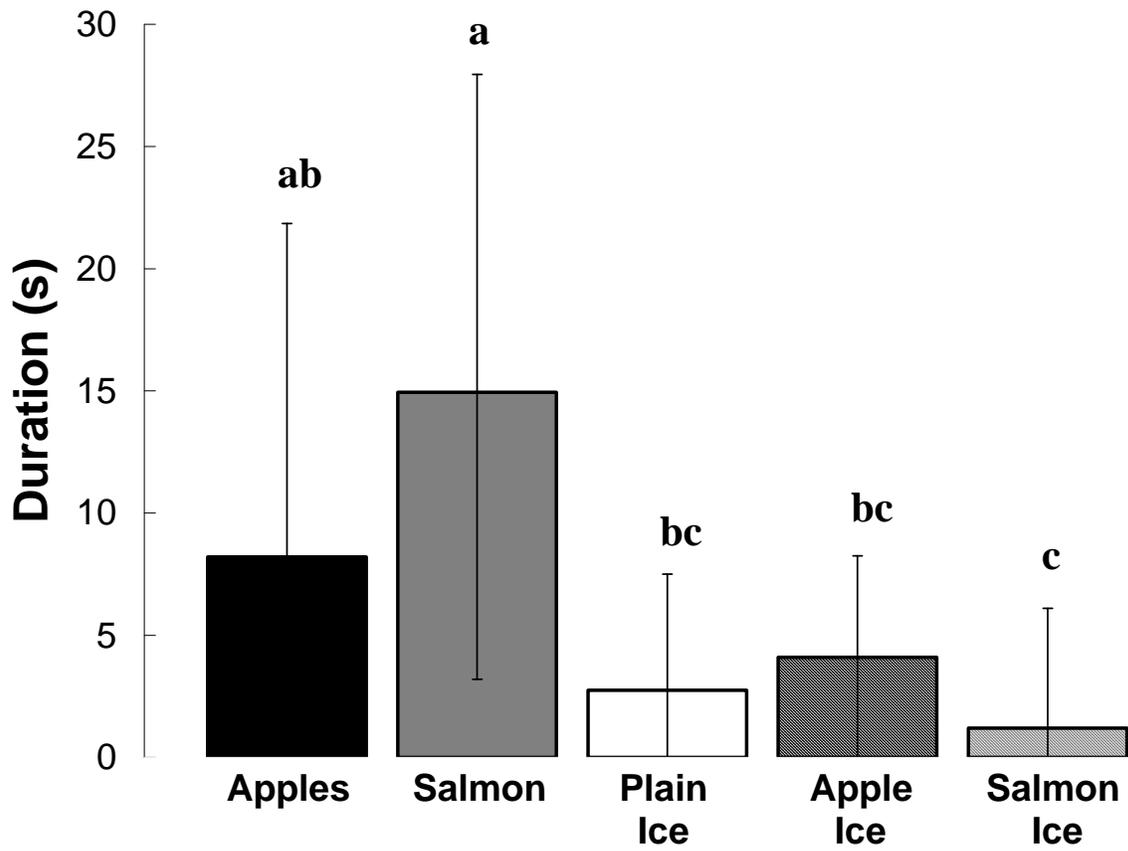


Figure 1. Median (\pm inter-quartile range) time bears (n=4) spent in non-contact investigation of five foraging options. Letters indicate differences ($P < 0.05$).

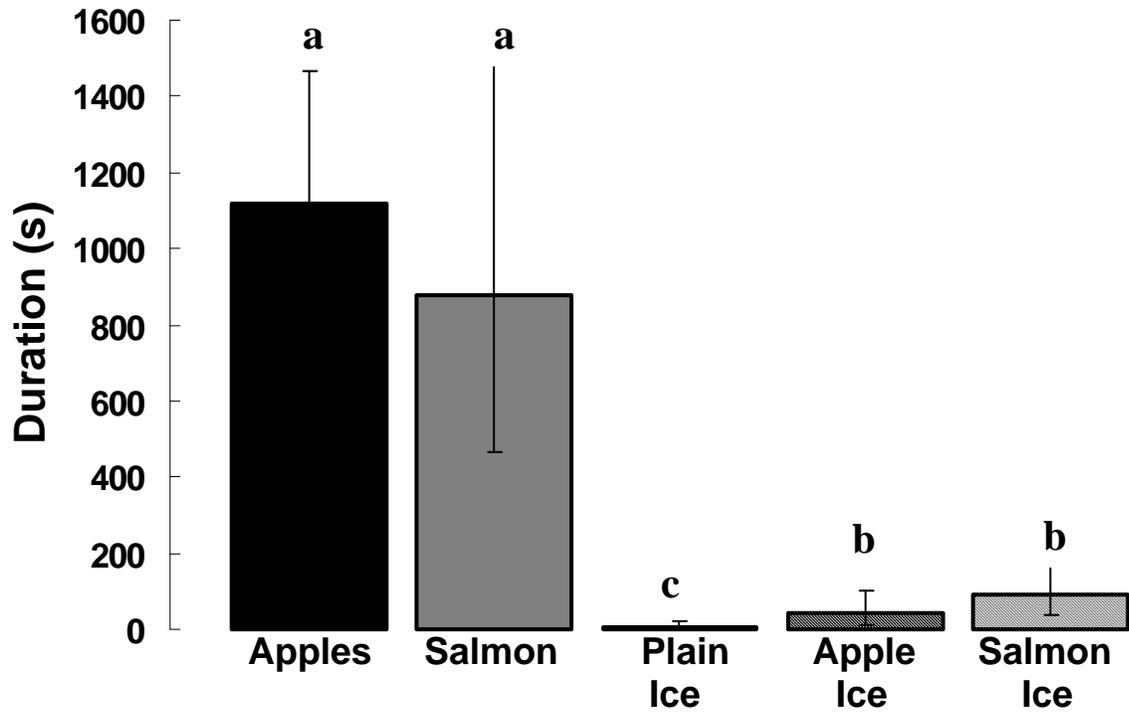


Figure 2. Median (\pm inter-quartile range) time bears ($n=4$) spent manipulating five foraging options. Letters indicate differences ($P<0.05$).

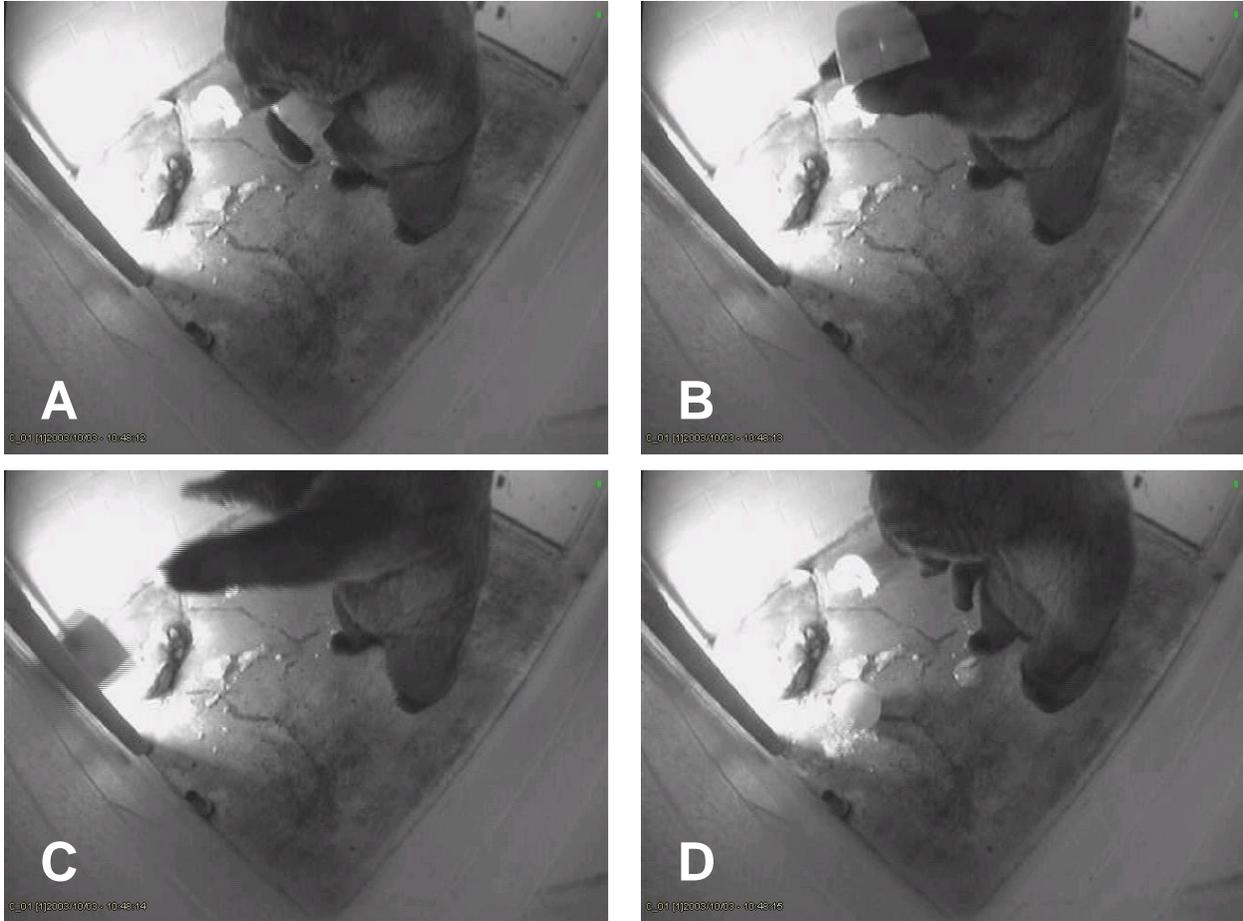


Figure 3. Video frames showing tactic employed by a male bear (“Bo”) to break open an ice block containing salmon. (A) Bo picks up ice block between forepaws and chin and stands upright; (B) Bo stretches out arms with ice block held between forepaws; (C) Bo tosses ice block against pen wall; (D) Bo investigates shattered ice block.

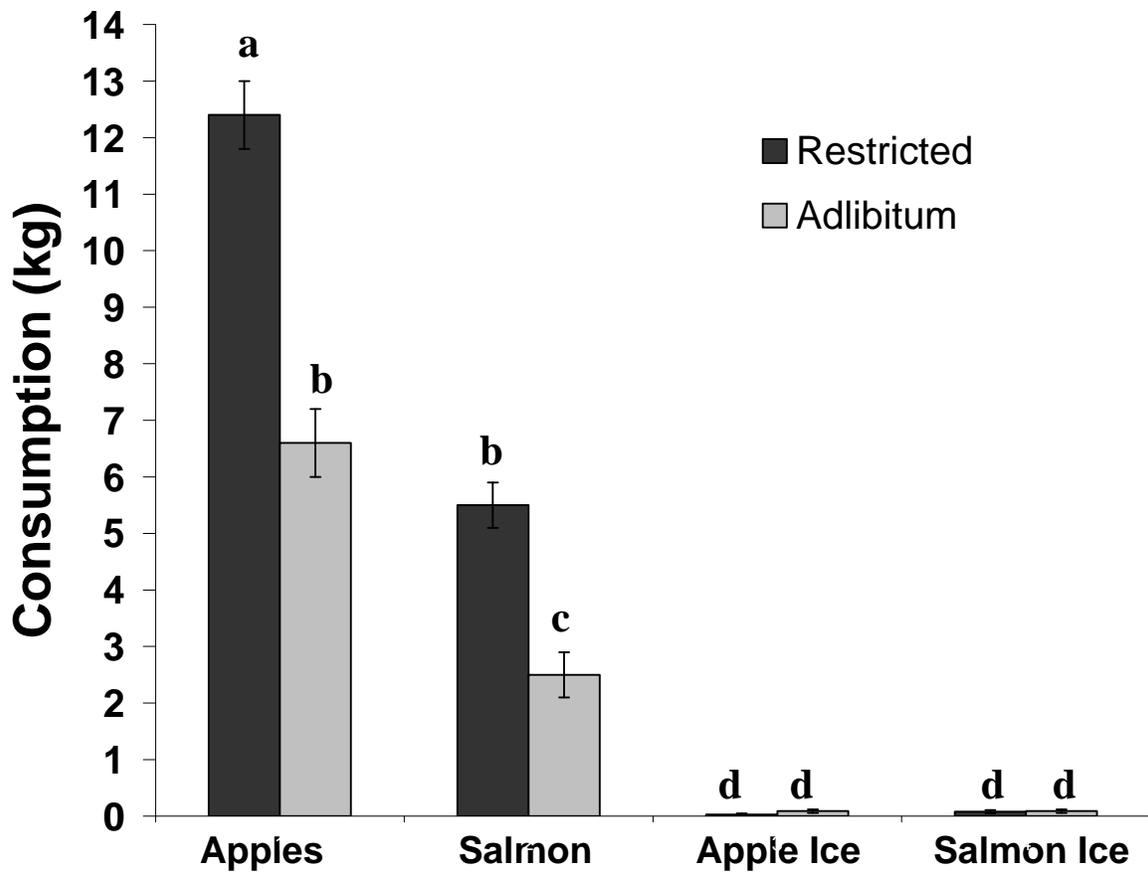


Figure 4. Mean (\pm SE) consumption of four food options (Apples, Salmon, Apples from ice, Salmon from ice) by bears ($n=4$) during application of two food treatments. Letters indicate differences ($P<0.05$) across food treatments and options.

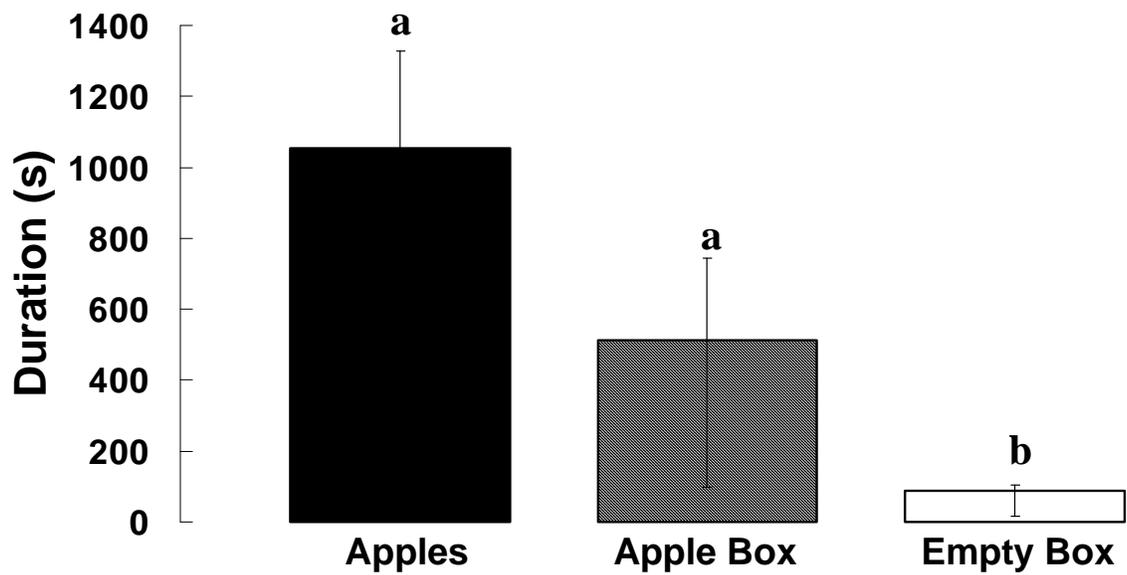


Figure 5. Median (\pm inter-quartile range) time bears (n=6) spent manipulating three foraging options. Letters indicate differences ($P < 0.05$).

CHAPTER THREE

TO WORK OR NOT TO WORK? SEX DIFFERENCES IN SUB-OPTIMAL FORAGING DECISIONS OF DOMESTIC FOWL

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ABSTRACT

Contrafreeloading occurs when animals choose to “work” for resources when more easily exploited resources of the same value are freely available. Previous studies suggest that there are sex differences in the foraging strategies of domestic fowl, with males preferring easily exploited food in pelleted form and females of egg-type strains preferring small food particles requiring greater effort to harvest (i.e., contrafreeloading). Laying hens are more likely to express cannibalistic and feather pecking tendencies when fed pelleted food than when fed the same food in small particulate form. To understand the apparent sex differences in contrafreeloading and

cannibalistic tendencies of domestic fowl, we conducted two experiments in which we manipulated sex hormones of hens. In a third experiment, we investigated sex differences directly, comparing contrafreeloading among adult hens and roosters. In each experiment, we provided two food types which varied in particle size in a contrafreeloading paradigm. Exogenous gonadal steroid treatment had no effect on contrafreeloading behavior, but early treatment with estradiol reduced total consumption by adult hens relative to treatment with androgens or vehicle (control). Females performed variably in regards to contrafreeloading, with Lohmann Brown hens showing strong tendencies and Lohmann LSL Lite and White Leghorn hens showing weaker tendencies toward the behavior. Males demonstrated behavior consistent with maximizing net energy gain. Varying the form of diet to include smaller particles that chickens can manipulate/investigate could be considered a form of enrichment to reduce unwanted behaviors in laying hens.

Keywords: Chickens, Contrafreeloading, Optimal foraging, Environmental enrichment

1. Introduction

Animal foraging decisions are influenced by a complex array of interconnected factors including physiological state, food availability and competition. It is often assumed that animals will act as maximizers, making choices that increase the ratio of reward to effort expended during foraging endeavors (MacArthur and Pianka, 1966, Stephens and Krebs, 1986). At least in captivity, however, animals will sometimes depart from an optimal foraging strategy by devoting time and energy to exploit resources that are challenging to acquire when the same resources are

simultaneously available in an easily exploited form. Termed contrafreeloading, this phenomenon has been documented in several mammalian and avian species in captivity (see Osborne, 1977 and Inglis et al., 1997 for reviews). Though contrafreeloading is expressed under numerous experimental paradigms, we do not have a clear understanding of why animals behave in this manner.

Contrafreeloading may represent an adaptive form of exploration where animals seek information about alternative resources through sampling. Information acquired during contrafreeloading bouts, when resources are abundant, could be applied during future foraging endeavors when reliable resources are depleted (Inglis and Ferguson, 1986). Whereas this behavior has obvious adaptive benefits in the wild, it would seem superfluous in captivity when animals are provided with food ad libitum. Yet some captive (wild and domestic) animals appear to retain a strong, internally driven motivation to explore and learn about environmental contingencies (Panksepp, 1998; Inglis, 2000), and a lack of opportunity to express this behavior may have negative emotional consequences or lead to the expression of abnormal behavior (Blokhuys, 1986; Clubb and Mason, 2007). Animals may be generally motivated to explore or generate cognitive challenges (Meehan & Mench 2007), or specifically to perform appetitive components of foraging behavior. A more complete understanding of factors underlying apparently sub-optimal foraging is called for.

In this paper, we examine food choice in domestic fowl (*Gallus gallus domesticus*) in relation to the phenomenon of contrafreeloading. Chickens are prime subjects for the study of contrafreeloading, as they are adept at foraging tasks, their natural feeding behavior involves

prolonged searching for unpredictable food items, and they are widely kept for production purposes so enhanced knowledge of their foraging behavior is useful for development of enriched housing systems. Contrafreeloading has been reported in both jungle fowl and domestic fowl (Schütz and Jensen, 2001; Lindqvist et al., 2002; Lindqvist et al., 2006). Though increased selection pressure for production traits (rapid growth and egg production) appears to have reduced the intensity of contrafreeloading behavior (Schütz and Jensen, 2001; Lindqvist et al., 2002; Lindqvist et al., 2006), domestic chickens will reliably explore and exploit sub-optimal foraging resources when more readily available foraging resources are present.

Previous studies suggest that there are sex differences in the foraging strategies of domestic fowl, with males preferring pelleted food that can be quickly consumed (Leone and Estévez, 2007) and females of egg-type strains preferring small food particles that are more costly to harvest over the same food in pelleted form (Newberry et al., in preparation). Laying hens are more likely to express cannibalistic and feather pecking tendencies when fed easily exploited food in pelleted form than when fed the same food in small particulate form (Bears et al., 1949; Newberry et al., in preparation). It is also notable that, whereas cannibalism is a common problem in laying hens, there appear to be no published reports of cannibalistic behavior by adult males (Newberry, 2004). If feeding on pellets does not fully satisfy the foraging motivation of laying hens, they may then be more likely to direct foraging pecks towards other pecking stimuli within the environment, such as the feathers and tissues of cage mates (Newberry, 2004; Newberry et al., 2007). Any new knowledge about the foraging preferences of laying hens could, thus, have important implications for the design of foraging enrichment programs aimed at reducing behavioral problems such as cannibalism and feather

pecking. In an effort to understand the apparent sex difference in cannibalistic tendencies of domestic fowl and its relation to exploratory behavior, we conducted two experiments in which we manipulated sex hormones of hens and compared their contrafreeloading behavior, based on their level of preference for foraging on small food particles in the presence of larger particles (pellets). In the third experiment, we investigated sex differences directly, comparing contrafreeloading among adult hens and roosters. The study was conducted in accordance with animal care and use guidelines approved by the Washington State University Institutional Animal Care and Use Committee.

2. Experiment 1: Whole versus ground pellets—Do circulating gonadal steroids influence contrafreeloading behavior?

In this experiment, we manipulated hormone levels in laying hens to investigate the hypothesis that sex differences in the propensity to contrafreeload arise from differences in circulating gonadal steroids. If testosterone contributes to the tendency of males to select rapidly-consumed food, we predicted that hens treated with testosterone would show a reduction in contrafreeloading behavior relative to control hens by consuming more food in whole pellet form than ground form. Based on the finding that estradiol promotes ground pecking by ovariectomized hens (Horne and Wood-Gush, 1970), we predicted that hens treated with additional estradiol would contrafreeload at a higher level than vehicle-treated control hens by consuming an increased proportion of ground pellets compared with whole pellets. Progesterone is associated with incubation and broodiness. Therefore, we predicted that hens treated with progesterone would exhibit reduced overall feed intake compared with control birds, and be less motivated to engage in contrafreeloading behavior. Based on a report by Hughes (1973) of an

increase in cannibalism when pullets were implanted with estradiol and progesterone compared with estradiol alone, we included an estradiol plus progesterone treatment in our experiment, predicting that this treatment would be associated with increased contrafreeloading relative to control hens.

2.1 Animals and housing

Female chicks of a strain selected for table egg production (Lohmann Brown) were obtained from a commercial hatchery (Featherland Hatchery, Cogburn, OR) and housed in wire-floored brooder units until 4 weeks of age, at which point they were transferred to enriched floor cages where they remained for the duration of the study. Each bird was marked with plastic leg bands to facilitate individual identification. Floor cages consisted of a main compartment measuring 91 cm x 91 cm x 100 cm (*l x w x h*) used to house 8 birds per cage, and an adjoining side compartment (30 cm x 91 cm x 100 cm) located to the right of the main compartment (separated by a wire mesh divider) used to isolate individual birds. Cage furnishings included a nest box (88 cm x 30 cm x 4 cm (*l x w x d*), 56 cm above the floor, main compartment only) and wood perch (85 cm x 5 cm in main compartment; 25 cm x 5 cm in side compartment) suspended 46 cm above the floor. A feed trough, spanning the full length of each cage compartment, hung on the cage front and a nipple drinker line extended along the back of each compartment. Wood shavings (6 cm deep) were provided as litter on the concrete floor. The side and back walls of each cage were constructed from solid metal flashing, and the top and front of each cage were constructed from open-air metal bars. This design allowed for visual isolation of each group from the birds in adjacent cages, and for visual surveillance of the birds by caretakers and researchers. Hens were provided with a conventional layer feed (Purina Mills® Layena®

SunFresh® Recipe pellets, St. Louis MO) and water ad libitum, and were kept on a 16:8 h light:dark cycle with lights on at 0600 h and off at 2200 h. Temperature was maintained at approximately 21°C and fluorescent lighting produced a light intensity of 72 ± 6.8 lx at the feed trough.

2.2 Hormone implants

For the purpose of a larger umbrella project, hens were randomly divided into 32 groups of eight and surgically implanted with an empty capsule (control) or with capsules of testosterone propionate (50 mg), 17- β estradiol (40 mg), progesterone (50 mg), or 17- β estradiol (25 mg) + progesterone (25 mg, Sigma-Aldrich, St. Louis MO). Each group was assigned to one of the four hormone treatments and comprised four randomly selected hormone-treated hens and four control hens. Birds were implanted twice during the study; initially at 16 weeks of age and again at 26 weeks of age. We constructed the implants using Silastic tubing (inner diameter 1.47 mm, outer diameter 1.96 mm; Dow Corning, Midland, MI) and pure crystalline hormone in powdered form: a) powders were packed into 5 mm (progesterone) or 10 mm (testosterone, estradiol) lengths of Silastic tubing (capsules); b) the ends of the capsules were closed with a piece of wood (cotton tip sticks); and c) capsules, except those containing progesterone, were sealed with Silastic medical adhesive silicone. Implants were placed beneath the skin on each bird's neck: a) a local anesthetic spray was applied to the skin surface; b) a small incision was created with a surgical scalpel; c) the implants were inserted; and d) the incision site was closed with a medical staple. After implantation, birds were returned to their home cage.

2.3 Design and methods

Eight randomly selected hens per treatment (total 40 birds) were subjected to 24-h and 5-min choice tests in which we offered two feed options requiring different levels of effort for consumption. Each bird was tested twice (at 24 weeks and 29 weeks of age) and all behavioral observations were made between 1300 and 1600h. Each test bird was removed from her group and isolated in the side compartment of her home cage. The wire mesh divider between compartments allowed birds to be physically separated but remain in visual contact with cage mates, so as to minimize stress associated with isolation from conspecifics. The two feed options were presented in a metal feed trough (24 cm long x 16 cm wide at the top x 12 cm deep, attached to the front of the isolation compartment) with a central divider, and a side extension on each end (extending 7.6 cm above the top of the feeder) to prevent birds housed in the main compartment from consuming feed from the test subject's feeder.

2.3.1 Foraging options

Given that it takes hens longer to consume an equivalent amount of mash feed (small, unpelleted feed particles) than pelleted feed (Vilarino et al., 1996; Aerni et al., 2000), we offered hens a choice of manufactured whole pellets (Purina Mills® Layena® SunFresh® Recipe pellets, approximately 6 mm x 2 mm, “free” food) and the same pellets in ground form (particles < 2 mm in diameter, “earned” food) in the divided feed trough during each test session. The ground food option was obtained by grinding whole pellets and sifting the resulting particles through a 2 mm sieve. Regrinding already pelleted feed allowed us to control for any changes in feed characteristics that might occur during the pelleting process (Carré et al., 1987). Thus, the two foraging options differed in physical make-up and, therefore, effort required for harvesting, but were identical in nutrient composition.

2.3.2 Twenty-four hour foraging choice tests

Hens were placed individually in the side compartment of their home cage, presented simultaneously with 300g of whole pellets and 300 g of ground pellets in the divided trough, and left in isolation for a 24-h period. The feed trough was then removed and the remaining feed on each side of the trough was collected and weighed. Any spillage was collected by feed type and included in the weights.

We balanced the position of the two choices (left or right) to control for social effects of neighboring birds and for the fact that lateralization of the visual process might induce asymmetry in the chicken's appraisal of the feed (Vallortigara et al, 1996).

2.3.3 Five minute foraging choice tests

Following the 24-h choice test, the birds were deprived of feed for 2 hours to stimulate feeding behavior. The hens were then presented with 100g of whole pellets and 100 g of ground pellets (in the same locations as for the 24-h test), and were observed continuously for 5-min. All observations were carried out between 1300 h and 1500 h each day. Remaining feed was then weighed and the hens were returned to the main cage compartment.

2.4 Measures

The weight of each food type consumed by the individual birds was calculated for both the 24-h and 5-min test session. For the 5-min choice tests, the number of pecks directed at each food type was recorded by direct observation using a Psion Workabout ® handheld computer

(PLC Inc., London, UK) equipped with The Observer ® Version 4.0 (Noldus Information Technology, Wageningen, The Netherlands). A peck was defined as a vertical movement of the beak directed toward a food source (Table 3). We used direct observation since Yo et al. (1997b) and Chagneau et al. (2006) found this method to be more reliable than automated recording for measuring pecking rhythms. Behavior data were collected by three observers (RTSM, SC & RCN) and inter-observer reliability was calculated to be $\geq 93.8\%$.

2.5 Statistical analysis

The difference in weight of each food type consumed by each bird (whole pellets – ground pellets) was compared using the Student's t-test. The difference in number of pecks directed at each option, and difference in effort expended to consume each option (pecks/g), were not normally distributed and so were converted to ranks and analyzed using the Wilcoxon signed-ranks test. These variables were also analyzed using the mixed linear model (Proc Mixed) of the SAS Institute (1999), with a compound symmetry covariance structure and trial (24 versus 29 weeks of age) as a repeated measure, to assess the effects of hormone treatment, trial and their interaction. We used the same model to assess these effects on the total food consumed (whole + ground pellets), total pecks and total effort expended. Pairwise means comparisons were made based on differences in least-squares means with Tukey adjustment. Significance level for all statistical computations was set at $\alpha=0.05$.

2.6 Results

During the 24-h tests, hens consumed more ground (mean \pm SE: 104 ± 6 g) than whole (62 ± 6 g) pellets (Student's t: $t=-3.71$, $n=40$, $P=0.004$; Fig. 6). In contrast, during the 5-min

choice tests, hens consumed more whole (6 ± 0.7 g) than ground (4 ± 0.3 g) pellets (Student's t : $t=2.49$, $n=40$, $P=0.015$; Fig. 7). Nevertheless, in the 5-min tests, hens directed more pecks at ground (median, IQR: 147, 247 pecks) than whole (47, 130 pecks) pellets (Wilcoxon signed-ranks: $S=-733$, $n=40$, $P=0.0002$; Fig. 8), thereby expending greater effort to consume ground (median, IQR: 36, 71 pecks/g) than whole (10, 15 pecks/g) pellets (Wilcoxon signed-ranks: $S=-1192$, $n=40$, $P<0.0001$; Fig. 9). We found no effect of trial (Mixed linear model: $F_{1,35}=2.93$, $P=0.096$), gonadal steroid treatment ($F_{4,35}=0.34$, $P=0.85$) or trial by treatment interaction ($F_{4,35}=0.30$, $P=0.874$) on the difference in the number of pecks directed at each food type during the 5-min tests. There was also no effect of trial (Mixed linear model: $F_{1,35}=0.98$, $P=0.329$), gonadal steroid treatment ($F_{4,35}=0.17$, $P=0.954$) or trial by treatment interaction ($F_{4,35}=0.39$, $P=0.813$) on effort expended (pecks/g) in consuming the two food types during the 5-min tests.

There was no effect of trial (Mixed linear model: $F_{1,35}=2.12$, $P=0.154$), gonadal steroid treatment ($F_{4,35}=0.86$, $P=0.499$) or trial by treatment interaction ($F_{4,35}=1.03$, $P=0.406$) on the difference in weight of each food type consumed during the 24-h tests. Similarly, there was no effect of trial (Mixed linear model: $F_{1,35}=0.48$, $P=0.493$), gonadal steroid treatment ($F_{4,35}=0.82$, $P=0.522$) or trial by treatment interaction ($F_{4,35}=0.14$, $P=0.967$) on the difference in weight of each food type consumed during the 5-min tests.

In considering the total weight of food consumed during the 24-h (mean \pm SE: 165 ± 5 g) and 5-min (9 ± 1 g) tests, and the total pecks directed at food (median, IQR: 217, 176 pecks) and total effort expended (46, 80 pecks/g) during the 5-min tests we found similar results. There was no effect of trial (Mixed linear model: $F_{1,35}=0.02$, $P=0.885$), gonadal steroid treatment

($F_{4,35}=0.74$, $P=0.570$), or trial by treatment interaction ($F_{4,35}=1.57$, $P=0.204$) on total consumption during the 24-h test. Similarly, there was no effect of trial ($F_{1,35}=3.95$, $P=0.055$), gonadal steroid treatment ($F_{4,35}=0.76$, $P=0.558$), or trial by treatment interaction ($F_{4,35}=0.56$, $P=0.693$) on total consumption during the 5-min test.

There was a significant effect of trial (Mixed linear model: $F_{1,35}=10.24$, $P=0.0029$) on the total number of pecks directed toward food, with more pecks occurring during Trial 1 (median, IQR: 266, 189 pecks) than Trial 2 (193, 158 pecks; Tukey adjusted t: $t_{35}=3.20$, $P=0.003$), but no effect of gonadal steroid treatment ($F_{4,35}=0.29$, $P=0.880$) or trial by treatment interaction ($F_{4,35}=0.64$, $P=0.636$). Despite the significant effect of trial on the total number of pecks directed toward food, there was no effect of trial ($F_{1,35}=0.04$, $P=0.85$) on effort (pecks/g) expended on food consumption during the 5-min tests; nor was there an effect of gonadal steroid treatment ($F_{4,35}=0.12$, $P=0.976$) or a trial by treatment interaction ($F_{4,35}=0.22$, $P=0.927$) on this variable.

3. Experiment 2: Whole pellets versus crumbles—Does exposure to gonadal steroids at hatch shape foraging behavior later in life?

Although the hormone implants did not affect the expression of contrafreeloading behavior in adult hens in Experiment 1, it is possible that early exposure to exogenous hormones could influence contrafreeloading behavior in adulthood. Exposure of chicks to exogenous estradiol before or soon after hatch is known to have long-term effects on the brain, with males showing more female-like characteristics in adulthood (e.g., Marx et al., 2004) and females showing more male-like characteristics (e.g., Adkins-Regan, 1999). Furthermore, egg yolk testosterone levels have been positively correlated with social rank in at least one bird species

later in life (Schwabl, 1993), indicating that level of early testosterone exposure can have long-term behavioral implications. Therefore, in this experiment, we investigated the effect of treatment of newly hatched female chicks with exogenous hormones on their contrafreeloading behavior later in life.

3.1 Animals, hormone treatments, and housing

For the purpose of a larger project, female chicks of a strain selected for table egg production (Lohmann LSL Lite; mean body weight \pm SE: 38 ± 1.0 g) were obtained from a commercial hatchery (Featherland Hatchery, Cogburn, OR). They were randomly divided into 32 groups of eight and injected within 24 h of hatch with a single dose (15 mg) of one of three hormones (testosterone propionate, dihydrotestosterone, 17- β estradiol) or safflower oil vehicle (control). Treatments were delivered by i.p. injection in a volume of 0.6 ml safflower oil. All chicks within a group were assigned to the same treatment, and groups were housed in the same manner described for Experiment 1. Thirty-two birds (8 per treatment) were randomly selected to be used in the current experiment.

3.2 Design and methods

Hormone treated and control birds were subject to a series of 24-h choice tests with two feed options having the same nutrient composition but requiring different levels of effort for consumption. Each bird participated in four trials, at 16, 17, 21 and 32 weeks of age, respectively. Methods were as described for Experiment 1 except that, in this experiment, birds were provided 200 g of whole pellets (Purina Mills® Layena® SunFresh® Recipe,

approximately 6 mm x 2 mm) and 200 g of the same diet purchased in crumble form (particles approximately 2 mm in diameter).

3.3 Measures and statistical analysis

The weight of each food type consumed by the individual birds was calculated by weighing remaining food after each 24-h test session. The weight of spilled food of each type was recorded and added to the weighed amounts. Statistical analysis was as described for Experiment 1.

3.4 Results

Across all treatments, birds consumed more whole pellets (median, IQR: 68, 47 g) than crumbles (36, 63 g) during the 24-h choice tests (Wilcoxon signed-ranks: $S=987$, $n=32$, $P=0.018$). There was an effect of trial on the difference in weight of each food type consumed (Mixed linear model: $F_{3,84}=11.98$, $P<0.001$; Fig. 10) but no effect of hormone treatment ($F_{3,28}=2.45$, $P=0.084$) or trial by hormone treatment ($F_{9,84}=1.63$, $P=0.119$). Hens demonstrated a preference for whole pellets over crumbles during Trial 1 (Tukey adjusted t : $t_{84}=4.28$, $P<0.0001$) and Trial 2 ($t_{84}=2.21$, $P=0.030$), no preference during Trial 3 ($t_{84}=1.06$, $P=0.291$) and a preference for crumbles over whole pellets during Trial 4 ($t_{84}=-2.99$, $P=0.004$). Birds spilled more crumbles than pellets over a 24-h foraging period (Wilcoxon signed-ranks: $S=-363.5$, $n=32$, $P=0.0023$). There was an overall effect of trial on the difference in spillage of each food type (Mixed linear model: $F_{3,84}=3.07$, $P=0.032$). However after adjustment for multiple comparisons differences between individual trials were no longer significant. There was no effect of hormone

treatment (Mixed linear model: $F_{3,28}=1.02$, $P=0.397$) or trial by hormone treatment interaction ($F_{9,84}=0.33$, $P=0.963$) on difference in spillage of each food type.

In considering the total food consumed there was an effect of hormone treatment (Mixed linear model: $F_{3,28}=7.31$, $P=0.0009$; Fig. 11), trial ($F_{3,84}=18.35$, $P<0.0001$; Fig. 12) and a trial by hormone treatment interaction ($F_{9,84}=2.08$, $P=0.040$; Fig. 12). There was also a significant effect of trial ($F_{3,84}=4.14$, $P=0.0087$) on total food spillage, with birds spilling more food in Trial 3 than in Trial 2 (Tukey adjusted t: $t_{84}=-3.36$, $P=0.006$).

4. Experiment 3: Social pairing—Does competition influence the willingness to work?

In Experiments 1 and 2, adult laying hens (24 weeks of age and older) exhibited a preference for small food particles over whole pellets. By contrast, it appears that males maximize energy gain to expenditure ratio, choosing food that can be quickly consumed (Leone and Estévez, 2007). Given the lack of exogenous gonadal steroid effects on contrafreeloading in Experiments 1 and 2, we compared contrafreeloading directly between adult males and females in Experiment 3. Additionally, we investigated the impact of social housing on contrafreeloading, given that our previous data were obtained from isolated birds. We predicted that, if competition resulted in some birds having reduced access to the feed trough, pairing would result in an overall shift preference towards increased consumption of pellets, which are more efficient to consume. Alternatively, if the birds preferred to feed together when housed together, we predicted that pairing would result in an overall shift towards increased preference

for small food particles (the most common preference of adult hens when isolated) versus whole pellets.

4.1 Animals and Housing

We used 24 adult (53 weeks of age) White Leghorn chickens (12 hens and 12 roosters). Females and males were housed separately in two floor pens measuring 1.73 m x 2.08 m x 2.44 m high, each with a three-rail wooden perch structure (1.07 m long x 1.22 m high at top rail) and wood shavings throughout (12 cm deep). Feed (Purina Mills® Layena® SunFresh® Recipe pellets) was provided ad libitum in a tube feeder (43.2 cm x 43.2 cm x 54.6 cm, 18.14 kg capacity; pan diameter 63.2 cm) and water ad libitum in a tube drinker (31.1 cm x 31.1 cm x 27.3 cm, 7.57 L capacity; pan diameter 48.3 cm) located in the center of each pen. The lights were kept on a 16:8 h light:dark cycle with lights on at 0600 h and lights off at 2200 h. Pens were located within a windowless, ventilated room with controlled temperature (approximately 22 °C) and fluorescent lighting.

4.2 Design and methods

Birds were provided the opportunity to forage on whole pellets (Purina Mills® Layena® SunFresh® Recipe) or ground pellets prepared as described in Experiment 1. Each bird was tested under two scenarios (individually and with a social companion) and all behavioral observations were made between 1300 and 1600 h. Experimental trials were conducted in test pens adjacent to their home pens, and having the same dimensions and features. Chain-link fences between pens allowed birds to be physically separated but remain in visual contact with pen mates, so as to minimize stress associated with isolation from conspecifics.

4.2.1 Foraging choice tests

Food preference tests (24-h and 5-min) were conducted in the same manner as described for Experiment 1 with slight modifications. During 24-h choice sessions each bird was presented with 600 g of both whole and ground pellets, via two round feeders (identical to those in the home pens) elevated above the pen floor (on a cement cinder block) to minimize contamination with shavings. During the 5-min choice sessions, each bird was presented with 300 g of both whole and ground pellets. Birds were initially tested individually and then as pairs (4 female-male pairs, 4 female-female pairs, and 4 male-male pairs).

4.3 Measures

The weight of each food type consumed (24-h and 5-min tests) and number of pecks directed toward each food type (5-min tests) by the individuals and pairs were collected in the same manner as described for Experiment 1. During pair tests, behavior data were collected by two observers simultaneously (one observer for each bird of a pair).

4.4 Statistical analysis

The difference in weight of each food type consumed by each bird (whole pellets – ground pellets) was compared using the Student's t-test. The difference in number of pecks directed at each option, and difference in effort expended to consume each option (pecks/g), were not normally distributed and so were converted to ranks and analyzed using the Wilcoxon signed-ranks test. These variables were also analyzed using the general linear model (Proc GLM) of the SAS Institute (1999), with a compound symmetry covariance structure to assess the effects

sex and/or pairing treatment and their interaction. We used the same model to assess these effects on the total food consumed (whole + ground pellets), total pecks and total effort expended. Pairwise means comparisons were made based on differences in least-squares means with Tukey adjustment. Significance level for all statistical computations was set at $\alpha=0.05$.

4.5 Results

4.5.1 Individual birds

During the 24-h tests, birds consumed more whole (mean \pm SE: 61 ± 14 g) than ground (21 ± 7 g) pellets (Student's *t*: $t=4.47$, $n=24$, $P=0.0002$). We found no effect of sex ($F_{1,23}=0.98$, $P=0.334$) on the difference in consumption of the two food types. Conversely, there was an effect of sex on total consumption over 24-h (GLM: $F_{1,23}=4.92$, $P=0.037$), with females (mean \pm SE: 119 ± 7 g) consuming more food than males (89 ± 12 g; Fig. 14).

During the 5-min tests, we found no effect of sex on the difference in consumption (GLM: $F_{1,23}=2.22$, $P=0.150$), difference in pecks ($F_{1,23}=0.13$, $P=0.727$), or difference in effort (pecks/gram) expended ($F_{1,23}=2.16$, $P=0.156$) between the two food options. There was a significant effect of sex on the total number of pecks (GLM: $F_{1,23}=32.58$, $P<0.001$) directed at food during the 5-min tests, with females pecking more than males (Tukey adjusted *t*: $t_{23}=5.65$, $P=0.0001$), and an effect of sex on the total effort (pecks/gram) expended ($F_{1,23}=17.69$, $P=0.0005$), with females working more than males ($t_{23}=4.19$, $P=0.0015$).

4.5.2 Paired birds

During the 24-h tests, birds consumed more whole (mean \pm SE: 183 \pm 13 g) than ground (39 \pm 14 g) pellets (Student's *t*: $t=7.42$, $n=12$, $P<0.0001$). We found no effect of pairing treatment (GLM: $F_{2,11}=0.32$, $P=0.734$) on food choice or on total consumption over 24-h (GLM: $F_{2,11}=1.04$, $P=0.392$). During the 5-min test session, birds consumed more whole (mean \pm SE: 7 \pm 1 g) than ground (2 \pm 1 g) pellets (Student's *t*: $t=2.55$, $n=12$, $P=0.027$). We found no effect of pairing treatment on total consumption (GLM: $F_{2,11}=0.80$, $P=0.478$), the difference in consumption ($F_{2,11}=0.19$, $P=0.831$) between the two food types, the difference pecks directed at each food type ($F_{2,11}=0.13$, $P=0.883$), or the difference ($F_{2,11}=0.24$, $P=0.790$) or total ($F_{2,11}=2.05$, $P=0.185$) effort (pecks/gram) directed at the food items. There was, however, a significant effect of pairing treatment on the total number of pecks ($F_{2,11}=5.49$, $P=0.028$) with female-female pairs demonstrating the most pecking behavior (Fig. 14) and male-male pairs the least (Fig. 14; Table 4).

5. General Discussion

We observed little consistency in foraging strategy between the three flocks of chickens utilized for this study. In Experiment 1, when hens were provided the choice between an effortful (small particle) or relatively effortless (large particle) requirement for food consumption, they showed preference for small particles over the same food in pelleted form. Under an equivalent paradigm, hens from both Experiments 2 and 3 tended to prefer pellets over the same food in small particulate form. These behavioral differences seem to have little to do with hormone or social pairing treatments employed during our studies, indicating that other motivational mechanisms may be influencing foraging decisions in domestic fowl.

5.1 Sex differences in foraging strategies

Contrary to prediction, our manipulation of exogenous gonadal steroids in laying hens did not have a pronounced effect on contrafreeloading behavior. Nevertheless, notable differences in the foraging tactics of roosters and hens are still apparent. When we presented roosters with the option of consuming whole and ground pellets, they reliably, and almost exclusively, chose pellets. When birds were paired, male-male pairs demonstrated the least food oriented pecking behavior during 5-min observation sessions as compared to female-female or female-male pairs. Roosters rarely interacted with food presented in small particulate form and showed clear preference for larger particles. Our findings are consistent with those of Leone and Estévez (2007), who suggest that males prefer food items that can be quickly consumed over more costly options.

Based on consumption data from 24-h exposure to food choices, and observational data collected during 5-min sessions, it is clear that hens sample both small and large particle options. In 5-min direct observation sessions, females made more total pecks to food items than males and expended greater effort (pecks/gram) in consuming food than males. When birds were paired, female-female pairs demonstrated the highest levels of food directed pecking behavior as compared to male-male or female-male pairs. Detailed studies of pecking behavior in pigeons (Zweers, 1982; Deich et al., 1984; Allan, 1992; Bermejo et al., 1994) and hens (Yo et al., 1997a) have lead to a general acceptance that pecking serves more complex functions than just grasping food.

A considerable portion of pecks directed toward food do not result in grasping particles for consumption and may actually be exploratory (Yo et al., 1997b; Martaresche et al., 2000; Chagneau et al., 2006). In broilers, Yo and colleagues (1997) found that two out of every three pecks directed at food did not result in grasping food particles. Many pecks (e.g. with closed beak) seemed to be movements that resulted in disturbance of the feed particles in the feeder rather than movements aimed at grasping food particles (Yo et al., 1997a). Hens in our study spilled more crumbles over a 24 hour time period than pellets. This difference may indicate that hens were exploring and searching among the crumbles as opposed to just grasping them for consumption. Spillage varied between trials, with more food spilled in successive trials. This trend might be indicative of a switch in manipulation for consumption to exploration or play.

Given our findings, hens appear to be motivated to explore and manipulate food particles of varying sizes. Feeding on pellets alone may not satisfy this motivation. If food options do not fully satisfy the foraging motivation of laying hens, they may be more likely to direct foraging pecks towards other stimuli within the environment, such as the feathers and tissues of flock mates (Blokhus, 1986; Newberry, 2004; Newberry et al., 2007).

5.2 What could hens gain from manipulating small food particles?

It has been suggested that domestic animals subject to intense pressure for production may contrafreeload less as they should be motivated to forage optimally and maximize energy gain (Schütz and Jensen, 2001). It is also plausible, however, that physiological demands of production may produce greater incentive to explore food of more variable quality. We suggest that laying hens may be motivated to manipulate mash and ground pellets for the opportunity to

explore individual particles (comprising different ingredients) that may be less distinct when food is pelleted.

Chickens are capable of discriminating and selecting out specific food particles during foraging bouts. This selection process is fast and accurate due to the precise visual and tactile capabilities of chickens (Hogan, 1984; Nir et al., 1990; Chagneau et al., 2006). Chicks are capable of distinguishing between food pellets that differ minutely in physical shape (Picard et al., 2000). Food image (visual) and structure (texture, hardness) are important to birds (Savory, 1979; Hamilton and Proudfoot, 1995; Picard et al., 1999) and could be the underlying basis for the development of food preferences. Hens that are highly motivated to forage and seek information about feeding contingencies will be likely to choose small particulate food over whole pellets because this food form allows for the expression of intricate foraging behaviors; birds have the opportunity to seek out, sort and select individual food particles from crumbles and ground pellets.

5.3 Differences in female behavior

While hens in Experiments 1 and 3 demonstrated clear preferences for ground and whole pellets, respectively, the preference of hens in Experiment 2 seemed to change with increased exposure to the two resources. Though hens in Experiment 2 initially demonstrated a preference for whole pellets, by the fourth trial their foraging choices had shifted to reflect a clear preference for crumbles. This apparent shift in preference was accompanied by a gradual loss of consumption of pellets and a gradual increase of consumption of crumbles. There are several possible explanations for the seeming inconsistency in the foraging choices of laying hens. First,

this variability may relate to strain differences. Contrafreeloading has been investigated in both jungle fowl and domestic fowl (Schütz and Jensen, 2001; Lindqvist et al., 2002; Lindqvist et al., 2006), and there is evidence that domestication and intense selection has reduced the intensity of this behavior in some breeds. We investigated contrafreeloading in three different strains of laying hens. There may be underlying genetic differences that control contrafreeloading tendencies but, at present, little is known about these characteristics.

Differences in the propensity of contrafreeloading between the birds used in our three studies could also be related to age. Hens in Experiment 1 were tested at 24 and 29 weeks of age, hens in Experiment 2 were tested four times between 16 and 32 weeks of age, and hens in Experiment 3 were tested at 53 weeks of age. Previous studies have tested wild and domestic fowl at ages ranging from three weeks (Lindqvist et al. 2006) to 37 weeks of age (Lindqvist et al. 2002). Whereas experimenters have reliably elicited contrafreeloading in domestic fowl in these age ranges, testing animals at 53 weeks of age falls out of this norm. Further investigation into age effects on contrafreeloading is needed. It is plausible that this behavior may be reduced with age. Younger animals have a greater need to explore and learn about environmental contingencies, whereas older animals may rely more on past experience. However, age differences would not explain the marked differences in contrafreeloading tendencies between the hens we utilized in Experiments 1 and 2, since these birds were tested at similar ages.

Social factors can be major modulators of food intake behavior in chickens (Nielson, 1999; Cloutier et al., 2002). Pairing birds in our third experiment may have decreased contrafreeloading by creating a more competitive atmosphere. Foraging data were very limited

for paired birds as birds were involved in a whole suite of social interactions during the 5-min test sessions; descriptive accounts are provided (Table 4). This would not explain the low levels of contrafreeloading expressed by individual birds during the first phase of our experiment. Moreover, Lindqvist et al. (2006) tested birds in pairs under a contrafreeloading paradigm, and they report no effect of pairing on contrafreeloading behavior. Interestingly, they paired male and female chickens for each trial, but did not measure sex difference in the performance of contrafreeloading. Birds were tested between 3 and 4 weeks of age, and there may not be apparent differences in contrafreeloading behavior at this age. If this is the case then it may be that contrafreeloading in males is diminished with age. Further investigation is needed to examine possible changes in contrafreeloading tendencies with age.

5.4 Initial behavior: 5 minute tests

During Experiment 3, we found it difficult to reliably evaluate pecking efficiency and food choice, because the majority of the roosters did not forage during our 5-minute session. To obtain a more complete understanding of pecking behavior, it would be necessary to observe the birds for longer bouts. Even though hens in Experiment 1 showed a strong preference for ground food over a 24 hour choice test, during the 5-min choice tests, these hens consumed more whole than ground pellets. This may reflect an attraction to larger particles after the short period of food deprivation we used to elicit foraging behavior. The first five minutes of behavior may, thus, primarily reflect compensatory feeding. The information primacy model predicts that animals prefer easily exploited food after a period of deprivation (Inglis and Ferguson, 1986; Inglis et al. 1997). Cowan (1977) described the behavior of rats recovering from food or water deprivation. Rats systematically sampled small amounts of food and then explored their familiar

surroundings. Partial recovery from deprivation apparently ‘disinhibited’ exploration. Food deprived animals will attend to the most immediate need (i.e. reducing hunger) before continuing with more general (i.e. information gain) needs (Woodworth 1958; Inglis 2000).

5.5 Hormones and consumption

Notably, though our hormone treatments did not contribute to marked changes in contrafreeloading behavior, treatment of birds at hatch in Experiment 2 did lead to changes in total consumption in adult animals. Hens treated with androgens maintained consumption levels similar to control animals whereas those treated with estradiol exhibited significantly reduced consumption levels. The fact that estradiol treatment altered consummatory behavior, but not contrafreeloading behavior per se, suggests that estradiol alone is not responsible for differences in food particle preference.

6. Conclusions

Contrafreeloading in laying hens suggests that, despite being selected for egg production and feed efficiency over many generations, hens retain elements of foraging behavior that evolved under natural conditions. Laying hens are motivated to investigate food particles of varying size and increased opportunities for food selection may lead to reductions in the occurrence of behaviors such as cannibalism and feather pecking. This is important from an animal welfare perspective because a better understanding of the motivational system underlying cannibalistic behavior is needed to facilitate its prevention without resorting to beak trimming. It is also relevant for the design of effective foraging enrichment programs that satisfy the exploratory motivation of hens. Varying the form of diet to include smaller particles that

chickens can manipulate/investigate could be a reasonable form of enrichment to help reduce unwanted behaviors.

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Table 3. What defines a peck? Identifying food directed pecks for evaluation of effort

A peck includes	A peck does not include
Vertical movement of the head in feeder where beak movement is directed toward feed	Horizontal movements of head in feeder where beak movement is not directed toward feed
Contact of the beak with the bottom of the feeder (may contain food particles)	Beak contact with parts of the feeder which do not contain food particles (e.g. sides, wire brackets etc.)
Opening beak and grasping food particles	Beak wiping where bird is not directing movement toward food

Table 4. Accounts of behavioral observations during 5-min food choice tests with pairs of birds

Pair #	Pair Type	Observer description of bird behavior
1	Female-Female	Female A chased female B away from the feeder containing whole pellets. Female B consumed water and then foraged in the litter (pecking and scratching) avoiding Female A.
2	Female-Female	Female C began feeding from the feeder containing ground pellets. Female D made several attempts to peck at the ground pellets, and female C responded with mild threats. Female D quit her attempts to reach the ground pellets and moved on to forage from the feeder containing whole pellets.
3	Female-Female	Female E made threats to female F when F attempted to access the feeders. F avoided E.
4	Female-Female	Female G chose to forage on ground pellets and made threats towards female H when she attempted to access the ground feed. Female H avoided female G and foraged from the feeder containing whole pellets.
5	Female-Male	The female began feeding from the feeder containing ground pellets, the male ate with her briefly but the female pecked his comb and chased him away. The male made several attempt to return to the ground feeder but was chased away by the female each time.

Pair #	Pair Type	Observer description of bird behavior
6	Female-Male	The male pecked a few times at the whole pellets while the female foraged in the litter (pecking and scratching). The female approached and pecked at the whole pellets briefly, and the two then both began foraging in the litter.
7	Female-Male	The male began eating whole pellets and moved around the feeder blocking the female's attempts to peck at the whole pellets. By the end of the observation, the female was successful in grabbing pellets and dropping them into the litter to peck at and eventually eat.
8	Female-Male	The male followed the female around the pen, mounting her and blocking her from pecking at the feeder containing ground pellets. The female then chose to forage from the feeder containing whole pellets and the male pushed her away. While the male pecked at the whole pellets, the female began foraging from the feeder containing ground pellets.
9	Male-Male	Male A consumed whole pellets while male B sat on the perch. The two then walked around the pen. Male B began to feed from the feeder containing whole pellets and male A hopped onto the perch.
10	Male-Male	Male C pecked at, picked up and carried shavings in his beak. Male D foraged in the litter (pecking and scratching). Both eventually pecked at whole pellets.

Pair #	Pair Type	Observer description of bird behavior
11	Male-Male	Male E made several threats directed toward male F. The two circled around each other. Eventually both pecked at whole pellets.
12	Male-Male	Male G blocked male H from accessing both feeders. Male G consumed whole pellets and male H was not successful in accessing either feed option.

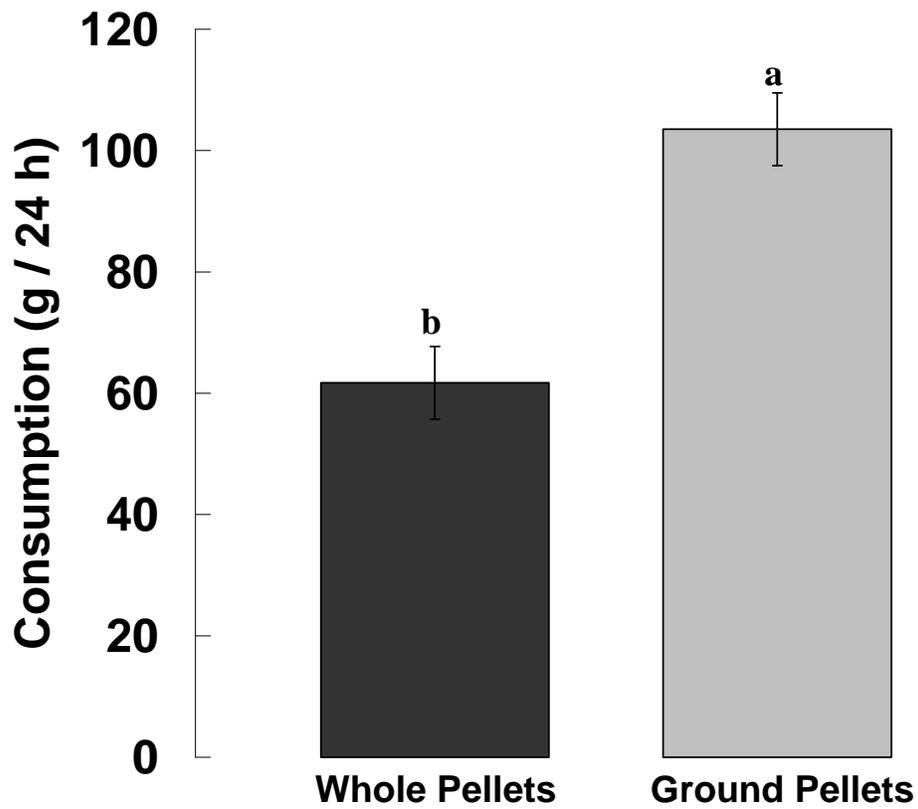


Figure 6. Mean (\pm SE) amount of whole and ground food pellets consumed over a 24 hour period. Letters indicate difference ($P < 0.05$).

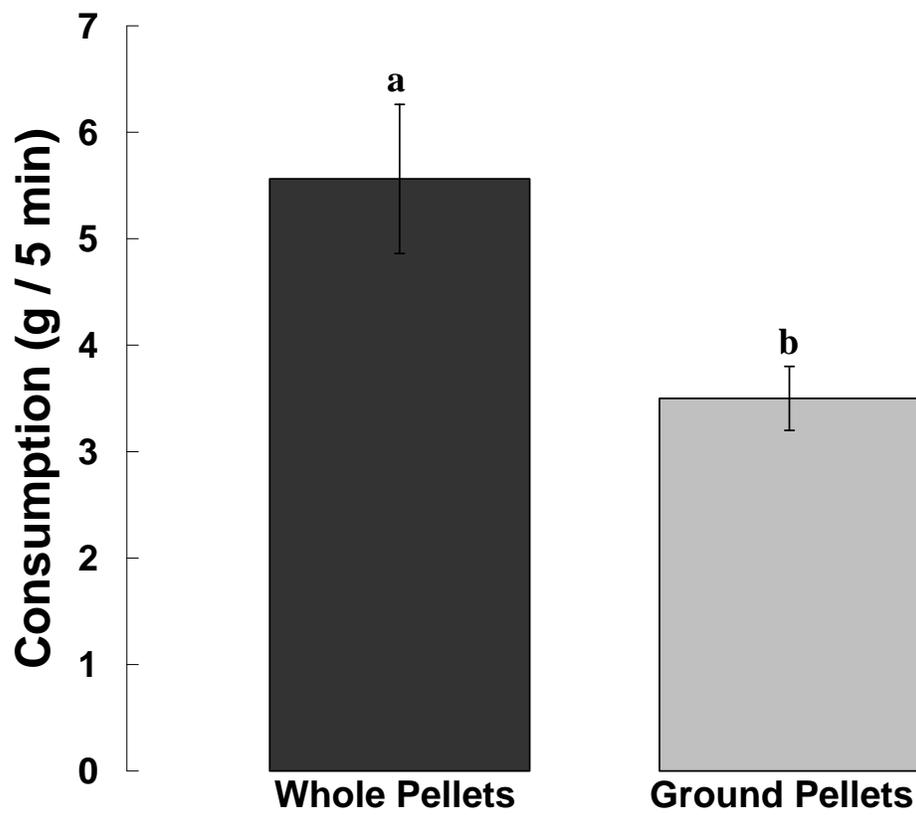


Figure 7. Mean (\pm SE) amount of whole and ground food pellets consumed per 5 minute test session. Letters indicate difference ($P < 0.05$).

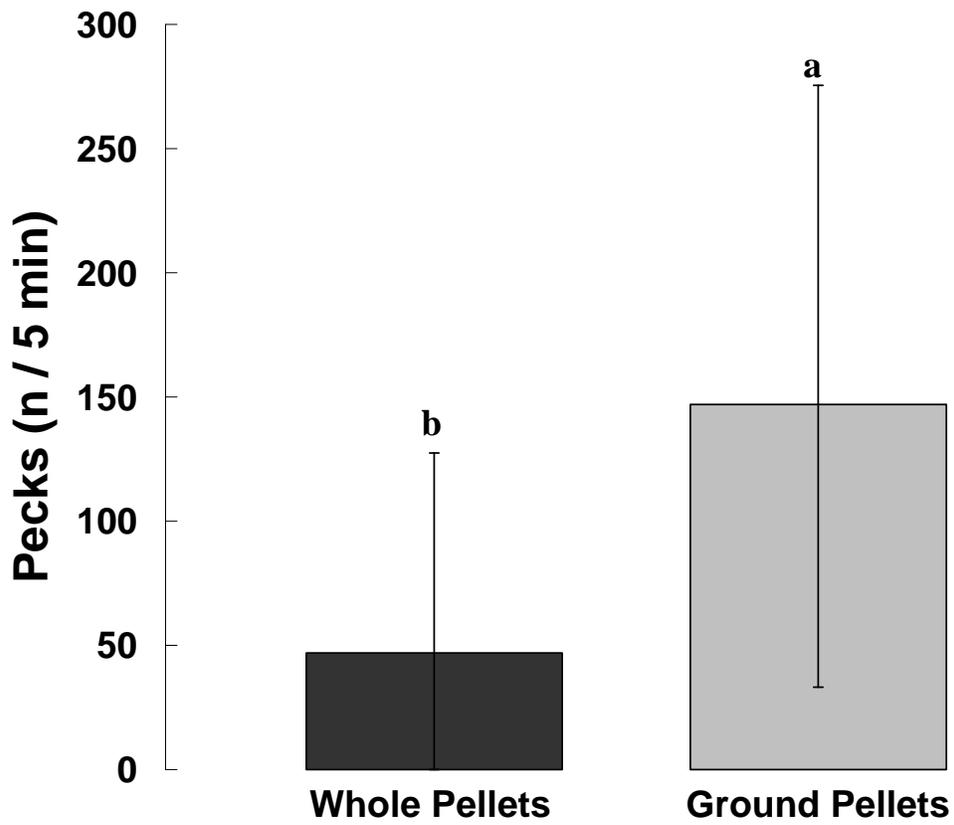


Figure 8. Median (IQR) number of pecks directed towards whole and ground food pellets per 5 minute test session. Letters indicate difference ($P < 0.05$).

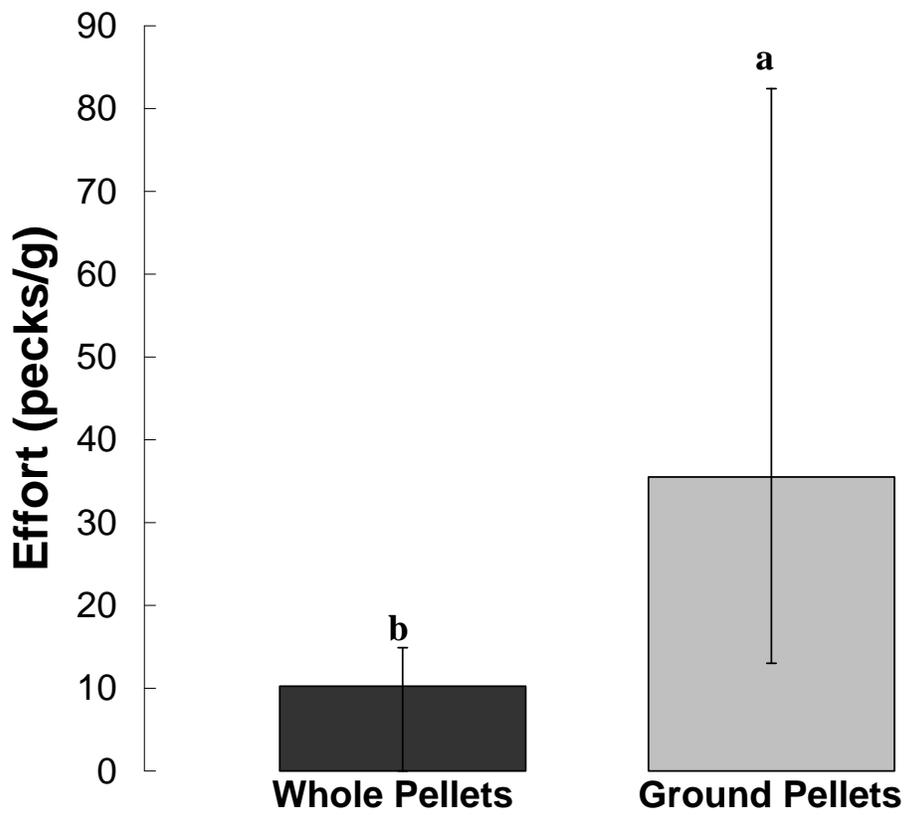


Figure 9. Median (IQR) effort expended (number of pecks/g of feed) for consumption of whole and ground food pellets per 5 minute test session. Letters indicate difference ($P < 0.05$).

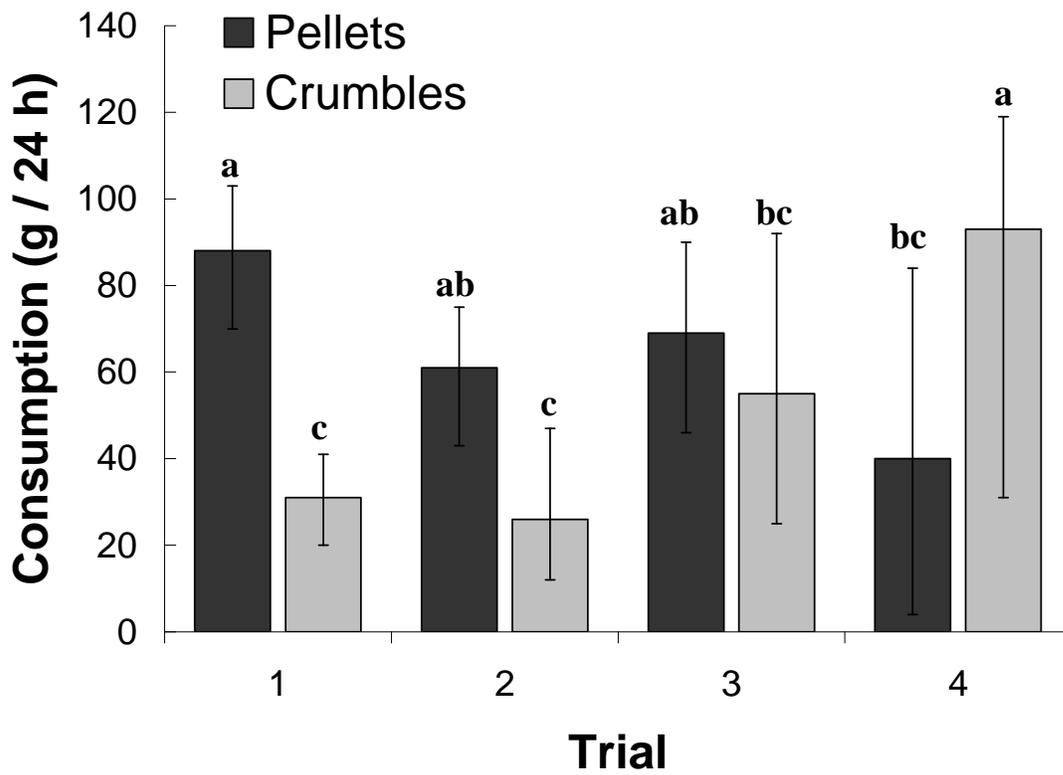


Figure 10. Median (IQR) consumption of pellets and crumbles during the 24-h test session. Letters indicate differences across foraging options and trials ($P < 0.05$).

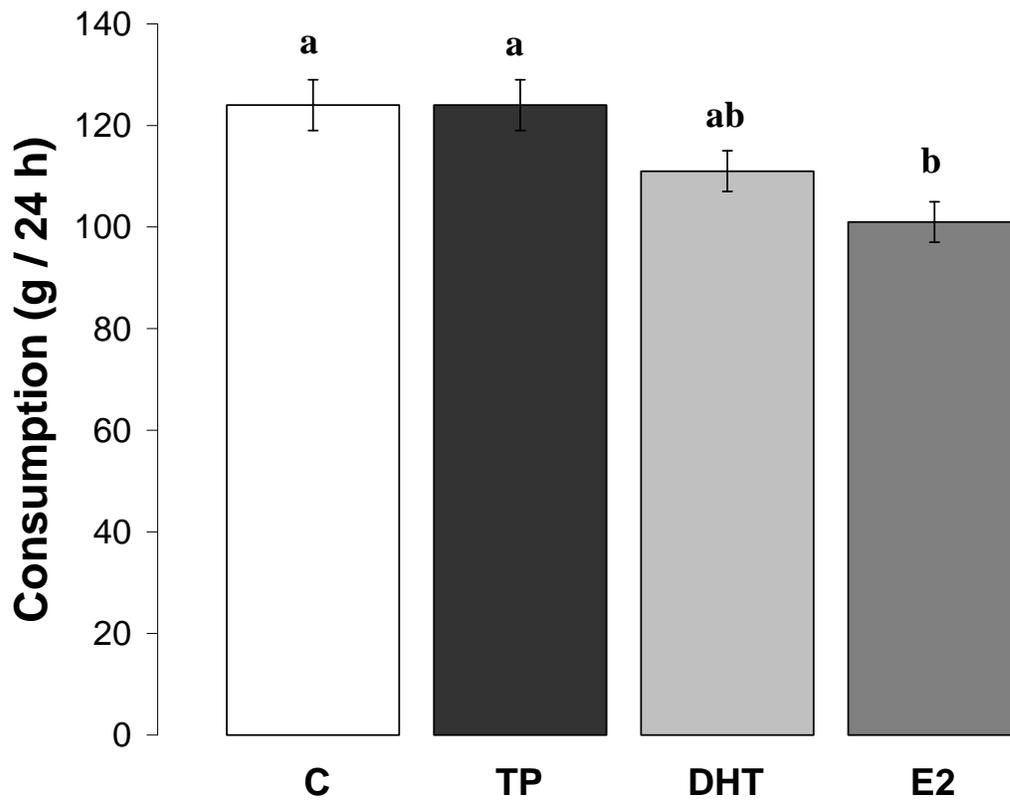


Figure 11. Mean (\pm SE) total food consumption during the 24-h test session by birds from each treatment: C = control, TP = testosterone propionate, DHT = dihydrotestosterone, E2 = estradiol. Letters indicate differences between treatments ($P < 0.05$).

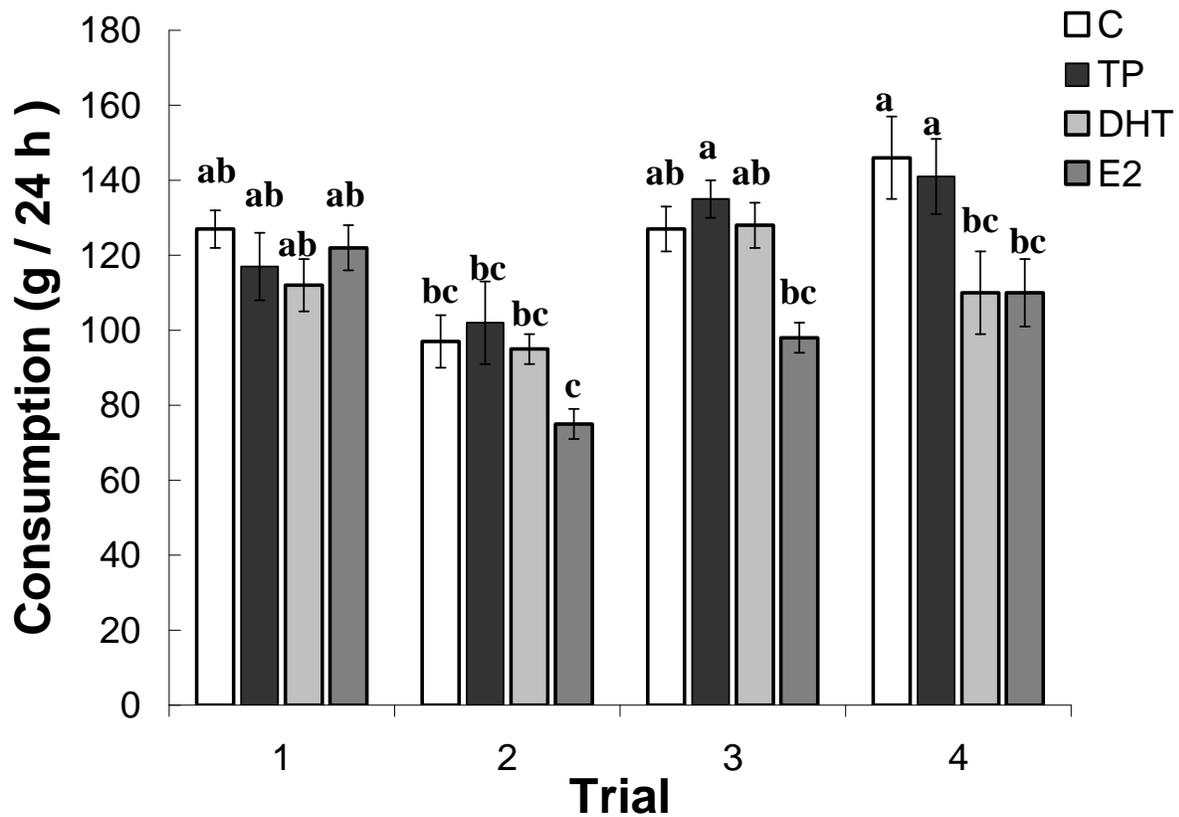


Figure 12. Mean (\pm SE) total food consumption during the 24-h test session by birds from each treatment (C = control, TP = testosterone propionate, DHT = dihydrotestosterone, E2 = estradiol) across the four trials. Letters indicate treatment differences across treatments and trials ($P < 0.05$).

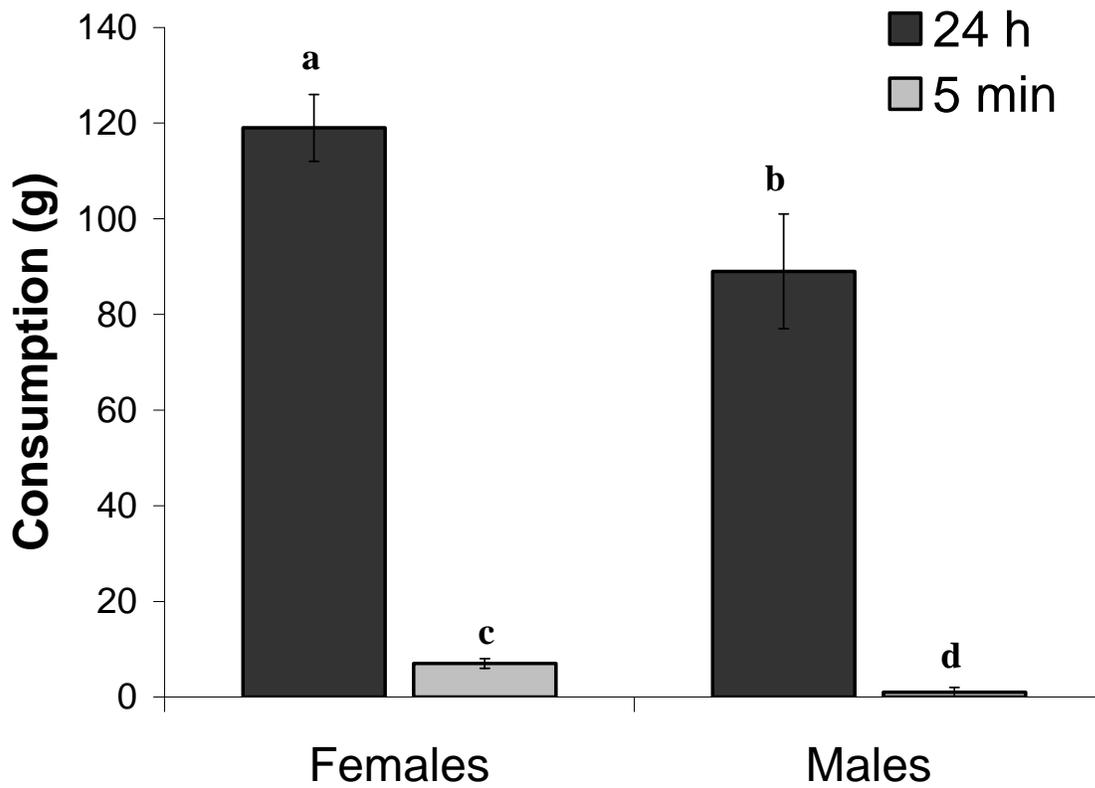


Figure 13. Mean (\pm SE) total food consumption during the 24-h and 5-min test sessions by females and males. Letters indicate differences among all bars ($P < 0.05$).

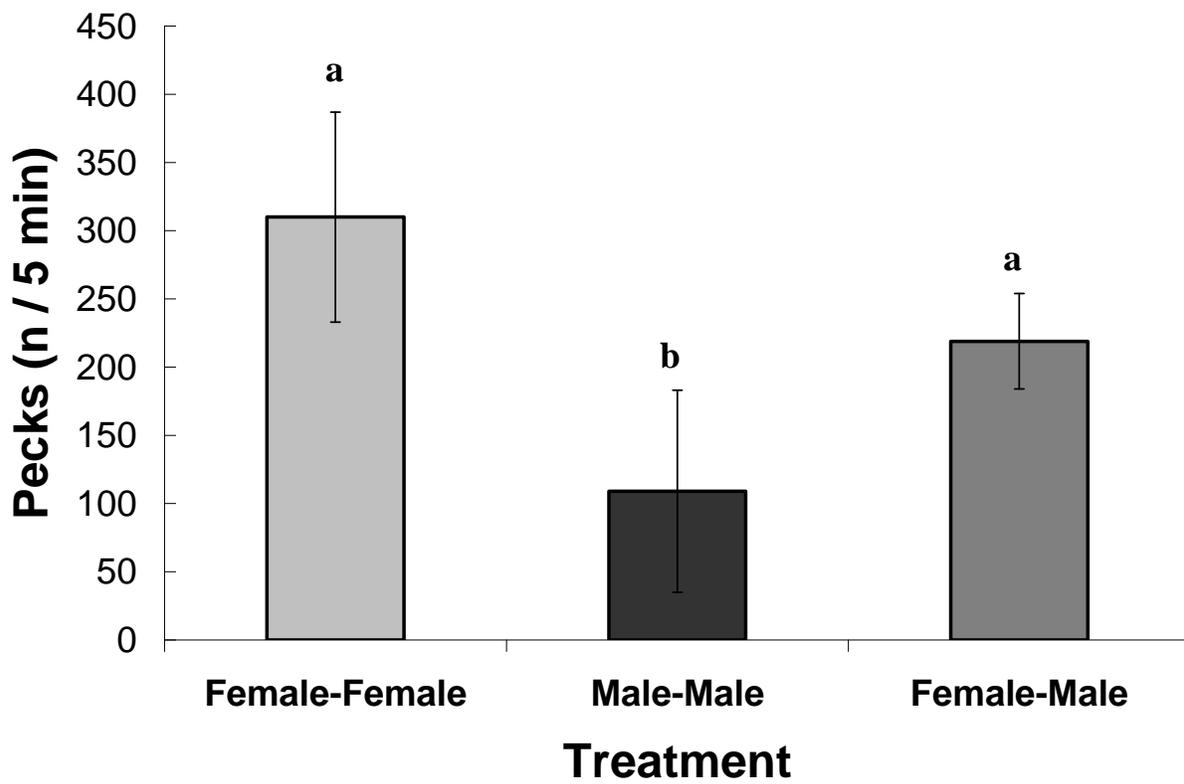


Figure 14. Mean (\pm SE) total pecks directed at food during 5-min test sessions by pairs of birds. Letters indicate differences between the treatments ($P < 0.05$).

CHAPTER FOUR

‘NEED’ OR ‘LUXURY’? MEASURING MOTIVATION FOR CONTRAFREELOADING IN LABORATORY MICE

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ABSTRACT

Contrafreeloading occurs when animals choose resources that require effort to exploit when identical resources are freely available. This seemingly anti-economical behaviour may reflect a motivation to perform appetitive foraging behaviour, whereby benefits accrue from gaining foraging skills and knowledge about different food resources. We predicted that ad libitum-fed laboratory mice would work for the opportunity to engage in contrafreeloading behaviour. We investigated this prediction utilizing a consumer demand approach, requiring mice to pay a ‘cost’ (climbing tubes) to gain access to foraging resources where they could engage in contrafreeloading. We constructed a test arena containing two climbing tubes, each leading to a foraging compartment, and systematically increased the incline of the tubes to manipulate the effort required to gain access to the compartments (0°, 22.5°, 45°, 67.5° and 90°). In exp. 1, one compartment contained hulled sunflower seeds (‘free’ food) and the other compartment contained a mixture of hulled and unhulled (whole) sunflower seeds (contrafreeloading

opportunity). To assess the importance of food as a lure for tube climbing, mice in Exp. 2 could climb tubes to access whole or empty sunflower hulls. Demand indices were calculated based on the number and duration of visits to each compartment. Mice exhibited a willingness to increase their effort to access all resources provided but were most strongly motivated to access a contrafreeloading opportunity (exp. 1) and empty hulls (exp. 2). These results suggest that mice actively seek opportunities to engage in behaviour that allows for information gain in relation to unfamiliar resources.

Keywords: mice, motivation, contrafreeloading, environmental enrichment, exploration, foraging

Many animals have evolved in stochastic environments where access to important biological resources is inherently contingent upon the performance of appetitive behaviour. In natural environments these animals encounter variation in the availability, accessibility, and palatability of resources on a regular basis and have been shaped by natural selection to cope with these challenges. An incentive to gather information about the environment through the performance of appetitive behaviour is crucial in assuring that an animal has the knowledge required to overcome unexpected challenges (Toates 1983; Hughes & Duncan 1988a; Inglis et al. 2001; Meehan & Mench 2007). For the wild animal, survival is dependent upon dynamic interaction with the environment and natural selection has provided the substrate, through neurological underpinnings in the seeking circuitry of the brain (Panksepp 1998; Spruijt et al. 2001), to incite exploration. It is not surprising, then, that the motivation to perform appetitive behaviour persists even among mammals and birds living in captive environments (Duncan & Kite 1989; Haskell et al. 1996; Sherwin et al. 2004).

A myriad of factors can influence the performance of behaviour and a variety of models have been proposed which attempt to explain how motivational systems operate (Lorenz 1950; Baxter 1983; Hughes & Duncan 1988a, 1988b; see Jensen & Toates 1993 for a review). Some motivational models concentrate on the external stimuli that trigger behaviour and draw on the assumption that appetitive behaviour is only performed as a necessary step in achieving the resources essential for survival (e.g. Baxter 1983). In these models, the functional consequences of behaviour are fundamental to its performance. In this sense, if an animal is housed in a setting where all of its physiological needs are provided for, the animal will have no need to express appetitive behaviour (Baxter 1983). Alternative motivational models acknowledge both internal and external stimuli that trigger behaviour and highlight the notion that animals may be motivated to perform appetitive behaviour itself apart from any immediate functional consequences the behaviour achieves (Lorenz 1981; Hughes & Duncan 1988a).

Given the complex motivational systems that animals have evolved in response to naturally volatile environments, many species may not be suited for a dependent lifestyle in captivity where basic resources are available with minimal effort on the part of the inhabitant (Hediger 1950; Poole 1998). Animal welfare could be jeopardized if captive environments do not provide opportunities for the execution of the behavioural sequences that animals are motivated to perform (Dawkins 1988; Morgan & Tromborg 2007), including both appetitive and consummatory components of complex behaviour (Hughes & Duncan 1988a, 1988b; Spruijt et al. 2001; Clubb & Mason 2003). An effort to pinpoint behavioural sequences that are important in terms of welfare has brought about the concept of 'behavioural needs,' whereby animals are

motivated to act out specific behaviour patterns even if the physiological needs which the behaviour serves are already fulfilled (Brambell et al. 1965; Hughes & Duncan 1988a, 1988b; Friend 1989; Dawkins 1990; Duncan 1998). Despite some controversy as to whether ‘need’ is an appropriate use of terminology (Jensen & Toates 1993; Cooper 2004) it is generally accepted that animals possess motivations apart from acquiring the resources immediately necessary for survival and reproduction (Hughes & Duncan 1988a; Poole 1992; Morgan & Tromborg 2007). These ‘behavioural needs’ are largely controlled by internal motivators that are present regardless of the environment the captive animal is provided (Hughes & Duncan 1988a, 1988b; Hughes et al. 1989). Thus, the performance of behaviours classified as ‘needs’ will persist no matter what types of resources are made available to the animal (Duncan & Kite 1989; Duncan 1998; Sherwin et al. 2004).

There are many examples where appetitive behaviour persists in satiated animals (Morgan 1974). Although in most behavioural sequences appetitive elements take place before consumption, this pattern is not invariable. A captive animal that has quickly consumed adequate food to meet nutritional requirements may still be motivated to perform the appetitive components (e.g. searching, hunting or processing) that normally precede food consumption (Duncan 1998; Inglis et al. 2001). For example, satiated primates will readily forage through brush piles to locate hidden food (Chamove 1982) and felids will exhibit hunting behaviour in the absence of any need to assuage hunger (Leyhausen 1979). Many animals will also perform seemingly frivolous feeding behaviour when consumption of the food is not contingent upon such behaviour (Swaisgood et al. 2003). For example, lion-tailed macaques have been observed to orally “peel” food items lacking protective casings (e.g. carrots) when such action is not

necessary for consumption (Smith et al. 1989). These observations support the argument that animals experience a ‘need’ to express behavioural components involved in food acquisition and processing that are associated with reward (Morgan & Tromborg 2007).

Contrafreeloading occurs when animals choose resources that require effort to exploit when identical resources are freely available at the same time. Though the phenomenon of contrafreeloading has been documented in a wide variety of species in captivity (see Osborne 1977 and Inglis et al. 1997 for reviews), reasons why the animals behave in this manner are poorly understood. Attempts to explain contrafreeloading have invoked the idea of ‘behavioural needs’ since this seemingly unnecessary activity may reflect an internal motivation (Gardner & Gardner 1988; Young & Lawrence 2003) which cannot be satisfied by mere consumption of resources (Jensen 1963; Hughes & Duncan 1988a; Jones & Pillay 2004). At first glance, contrafreeloading appears to conflict with predictions arising from evolutionary theory regarding behavioural economics. It is reasonable to expect animals to conserve energy when easily obtained resources are available and one might anticipate selection against behaviour that apparently “wastes” energy (Poole 1992). However, contrafreeloading may result from a motivation to perform foraging behaviour (Gardner & Gardner 1988) invoked by the seeking system (Panksepp 1998; Inglis 2000), thereby providing animals with the opportunity to experience reward from sampling. Animals may choose to work more than they need to if, by doing so, they improve their subsequent foraging skills (Chamove et al. 1982) enabling them to gain reward from exploiting alternative resources (Bean et al. 1999; Inglis et al. 2001; Swaisgood 2007). Energy spent obtaining information about alternative foraging resources could be recompensed by more efficient intake in the long run.

Identifying behaviours that may constitute ‘needs’ to captive animals is not a trivial problem but an understanding of the perceived importance of a behaviour to an animal can be gleaned from measures of how strongly the animal is motivated to perform that behaviour (Dawkins 1983; Mason et al. 2001; Jensen et al. 2004a; Sherwin 2007). Behavioural approaches borrowed from human microeconomics are being adopted for this purpose (Lea 1978; Dawkins 1983; Cooper 2004; Kirkden & Pajor 2006). A consumer demand approach, which requires an animal to pay a ‘cost’ to gain access to a resource, has proved useful for quantifying motivational strength for a broad range of species (e.g. broiler breeders-Savory et al. 1993; pigs-Matthews and Ladwig 1994; laying hens-Foster et al. 1997; mink-Cooper & Mason 2000; calves-Holm et al. 2002; rats-Ladewig et al. 2002; foxes-Hovland et al. 2006). Assorted methods for imposing costs on animals have been utilized, including operant tasks such as pressing levers (e.g. Sherwin and Nicol 1996), pecking keys (e.g. Sumpter et al. 1999) and pushing panels (e.g. Holm et al. 2002), or more complicated behaviours such as squeezing through narrow gaps (e.g. Nicol 1987), traversing water (e.g. Sherwin and Nicol 1995), lifting weighted doors (e.g. Mason et al. 2001) or pulling rubberized chains (e.g. Hovland et al. 2006). By increasing the effort required to gain access to a resource it is possible to estimate the strength of motivation towards and, therefore, perceived importance of, that resource to the animal (Lea 1978; Dawkins 1990; Mason et al. 2001; Sherwin et al. 2004). When faced with increasing costs for accessing resources, animals will persist in exploiting behavioural opportunities they perceive as important and cease efforts to exploit opportunities they perceive as relatively unimportant. In this sense, ‘necessities’ continue to be attained despite increasing costs and ‘luxuries’ are only attained when costs are minimal (Dawkins 1990; Bubier 1996; Kirkden et al. 2003).

Though contrafreeloading has been described as a ‘behavioural need’ (Gardner & Gardner 1988; Hughes & Duncan 1988a, 1988b; Poole 1992; Jones & Pillay 2004), little is known about motivation in relation to the performance of this behaviour. Some level of motivation for contrafreeloading exists, or it would not persist so readily in captive species. To date, however, there have been no published experiments designed to test the strength of motivation of animals to contrafreeload. In this paper, we explore contrafreeloading behaviour in laboratory mice (*Mus musculus*) to advance understanding of the foraging choices of these long-established research subjects and to assess the strength of their motivation to gain opportunities to contrafreeload. Laboratory mice are known to demonstrate contrafreeloading behaviour (Pallaud 1971) although little attention has been given to contrafreeloading in this species in recent literature. Mice are prime subjects for the study of contrafreeloading as they are adept at foraging tasks, their natural feeding behaviour involves prolonged searching for unpredictable food items, and they are widely kept for research purposes so enhanced knowledge of their foraging behaviour is useful for development of enriched housing systems.

A number of papers report the use of a consumer demand approach to examine motivational tendencies in laboratory mice. These include tests of motivation towards a variety of resources: nesting material (Roper 1973, 1975), food pellets (Sherwin & Nicol 1995, 1996; Sherwin 1996), visual access to a conspecific (Sherwin 1996; Sherwin & Nicol 1996), additional space (Sherwin 1996, 2003, 2004; Sherwin & Nicol 1996, 1997), opportunities for locomotion (Sherwin 1996, 1998, 2003; Sherwin & Nicol 1996), ‘toys’ (Sherwin 1996; Sherwin & Nicol 1996), burrowing substrate (Sherwin et al. 2004), a brief aggressive encounter (Fish et al. 2002)

and the opportunity to leave an enriched cage for an empty cage (Sherwin 2007). The predominant method of imposing costs in these studies is lever pressing (e.g. Roper 1973; Sherwin 1996-2007). Alternative costs include traversing water (e.g. Sherwin & Nicol 1995) and nose pokes through holes in an operant chamber (e.g. Fish et al. 2002).

We conducted two experiments utilizing a consumer demand approach to assess the strength of motivation of mice to engage in contrafreeloading, employing a novel method for imposing costs not previously employed in consumer demand studies. We hypothesized that reward gained from exploiting food from alternative sources motivates mice to contrafreeload, predicting that (1) mice would work for the opportunity to contrafreeload and (2) mice would defend access to such opportunities. To our knowledge, this is the first study to examine motivational strength in the context of contrafreeloading, providing insight into the question of whether contrafreeloading constitutes “luxury” behaviour performed only when food choices are easily accessible or whether mice actively seek opportunities to engage in contrafreeloading behaviour and are willing to make trade-offs to do so.

EXPERIMENT 1: WILL MICE WORK FOR AN OPPORTUNITY TO CONTRAFREELOAD?

Methods

Animals and Housing

We utilized 28 experimentally naïve female mice (C57BL/6J) between the ages of 3 and 21 months. Due to aggressive interactions between males, females were selected for study because they are more easily housed in social pairs (Van Loo et al. 2001). We housed the mice in pairs in standard mouse cages (24 cm x 14 cm and 13 cm high) with CareFRESH® bedding (4 cm deep; Absorption Corp, Ferndale, WA) and a red-tinted plastic ‘Mouse House’ (triangular 11.4 cm long walls x 6.35 cm high; Tecniplast USA, Exton, PA). Soiled bedding was replaced during cage cleaning once a week. Mice were provided ad libitum access to pelleted feed (Harlan Teklad Laboratory Rodent Diet, Madison, WI) and tap water through a stainless steel wire lid that covered each cage. All cages were located in a windowless, climate-controlled (21-23 °C, humidity 25-45%) room. The room was kept on a reversed 14:10h light:dark cycle with fluorescent lights automatically turned on at 2200h and off at 1200h and a dim red incandescent light (40 watts) switched on during dark periods to allow observation of the animals during their active period. All procedures were conducted in accordance with animal care and use guidelines approved by the Washington State University Institutional Animal Care and Use Committee.

Apparatus

The test arena was a clear plastic rat cage (43 cm x 22 cm and 20 cm high) with no bedding, containing two straight rodent climbing tubes (26 cm x 5 cm; S.A.M.® Bubble-Toob-A-Trail) each ending at a resource compartment (14 cm x 15 cm x 9 cm high; S.A.M.® Lookout Tower, Penn-Plax, Inc., Hauppauge, NY). A clear acrylic (plexiglass) lid was used to cover the open areas of the test arena to prevent mice from escaping. The design enabled mice to climb through the tubes to gain access to resources within the compartments. The arena was washed between mice to remove scent marks.

Foraging Options

Confectionary sunflower seeds were provided in different forms in the two compartments of the test apparatus. One compartment was supplied with “free food” (4 g of sunflower kernels without hulls) and the other compartment contained a “contrafreeloading opportunity” (mixture of 2 g of whole sunflower seeds with hulls and 2 g of sunflower kernels without hulls). No foraging options were provided outside of the compartments. We acquired both whole and hulled forms of sunflower seeds from the same batch from one manufacturer (Nature’s Nuts™, Chuckanut All Natural Products, Corvallis, OR) to assure uniformity in moisture level and nutritional content (crude protein (min.) 14%, crude fat (min.) 25%, crude fiber (max.) 31%) which can vary between crops. Following standard protocol for the animal facility, all seeds were autoclaved for 15 minutes at 121°C prior to being brought into the mouse room. We wrapped the seeds in aluminium foil for autoclaving, which roasted the seeds, but left kernels, and hulls around kernels where present, intact.

Training Sessions

Experiment 1 comprised a series of training sessions in the test arena followed by test sessions. The goal of the training process was to familiarize mice with 1) the test apparatus, 2) sunflower seeds as forage, 3) the skills necessary to climb through tubes, and 4) the location of the foraging options. For training sessions, 25 g of standard feed pellets (5 pellets) were included with the foraging option in each compartment to provide an element of familiarity.

Given that the literature indicates that C57BL/6 mice readily acquire spatial discrimination tasks (Ammassari-Teule et al. 1993; Paylor et al. 1993; Fordyce et al. 1995; Stavnezer et al. 2002; Delcasso et al. 2007) and demonstrate greater ability at these tasks than other strains of mice (Ammassari-Teule et al. 1993; Paylor et al. 1993; Fordyce et al. 1995; Mihalick et al. 2000; Brooks et al. 2005), we were confident that the mice were capable of learning the location of the different foraging options provided in our experiments. As an added measure, the tubes leading to the foraging compartments were marked with either a dark blue (near black) or light yellow (near white) ring to serve as a visual cue to the location of each foraging option. Mice are capable of making such colour discriminations (Jacobs et al. 2004, 2007). The locations of each resource as well as the colour markers were randomized through a Latin Square design to control for location and colour preference. The location and colour marker for each foraging choice was consistent for each mouse (the same for all training and testing sessions) but balanced between mice.

On the first day of training, the two tubes were placed parallel with the floor of the test arena (0°) to allow mice to explore each tube and compartment with minimal effort. Over the next six consecutive days of training, the angle of the tubes was systematically increased so that by the seventh day of training the tubes were perpendicular to the floor of the test arena (90°) requiring a vertical climb to access the foraging resources in the compartments. Mice were allowed to explore the tubes and foraging compartments for 10 minutes per day. They were not excluded from the experiment if they did not demonstrate proficiency in climbing a vertical tube because the main assessment measure of the experiment was motivation to access foraging opportunities and individual variation was expected within the sample.

Test Sessions

Once mice were familiarized with the apparatus, test sessions were conducted to quantify the amount of work each mouse was willing to expend to gain access to different foraging choices. Test sessions spanned five consecutive days. On day 1 of testing the tubes leading to each foraging compartment were placed parallel (0°) to the floor of the test arena. On each successive day the angle of the tube was increased by increments of 22.5° per day (22.5° , 45° and 67.5° for days 2, 3 and 4; respectively) so that by day 5 of testing the tubes were perpendicular (90°) relative to the floor of the test arena. Mice were allowed to explore the tubes and foraging compartments for 10 minutes per day for 5 consecutive days. For experiment 1, the completion of one trial (trial #1 = 5 sessions) was followed by a replicate trial (trial #2 = 5 sessions) so that each mouse was tested for a total of 10 consecutive days.

Measurements

Each 10-minute test session was video recorded for later analysis using The Observer $\text{\textcircled{R}}$ 4.0 program (Noldus Information Technology, Wageningen, The Netherlands). Videos were numbered in a manner that blinded the observer to the identity of each mouse during video playback. Three observers scored the tapes in a random order. Tests of inter-observer concordance indicated that reliability of data scoring was $\geq 95.3\%$ between observers. We recorded the maximum incline each mouse was willing to climb to access the foraging resources as well as the number of visits and the duration of time spent in each compartment.

Calculation of Strength of Motivation

A review of the literature reveals careful consideration and debate as to which measures borrowed from human economics have valid application to studies of animal motivation (e.g. Kirkden et al. 2003; Warburton & Mason 2003; Cooper 2004; Kirkden & Pajor 2006). There are positive and negative attributes to each measure, in terms of practicality and interpretation, so we chose to take an inclusive approach by considering the five most commonly adapted measures of demand. We considered three characteristics of demand functions ('Price Elasticity of Demand,' 'Intensity of Demand' and 'Consumer Surplus,') and two measures of energy expenditure ('Total Expenditure' and 'Reservation Price') in our assessment of the motivation of mice to access the foraging options.

We generated demand functions by plotting the relationship between visit price and the number and duration of visits to each resource compartment. To create straight line relationships as required for analysis of demand functions (Lea 1978), we log transformed all of the data points by adding 1.0 (to avoid excluding zero values) and taking the base 10 logarithm. Regression lines were calculated for each individual and mean regression lines were generated from the individual measures (n=28) to allow comparison between resources.

'Price Elasticity of Demand'

The slope of the regression line generated from a demand function is termed the elasticity coefficient. It has been argued that the elasticity coefficient represents the relative strength of

motivation for a resource (Lea 1978; Dawkins 1990; Matthews & Ladewig 1994; Mason et al. 2001; Sherwin 2007). If a resource is valued by an animal, interaction with the resource will remain fairly constant in spite of increasing costs and the elasticity coefficient will be close to zero (inelastic). In contrast, if the resource has little value to an animal, interaction with the resource will decrease with increasing costs and the elasticity coefficient will be close to one (elastic).

'Intensity of Demand'

The intensity of demand is ascertained from the Y-intercept of the regression line of a demand function (Dawkins 1990; Sumpter et al. 1999; Holm et al. 2002; Jensen et al. 2004b). The Y-intercept of the regression line indicates the intensity of an animal's response for a resource when there is no cost for accessing that resource. When comparing the demand functions for two or more resources, if the elasticity coefficients (slopes) are equal, a higher Y-intercept indicates the animals are more highly motivated to access a resource across the range of costs examined (Dawkins 1990; Holm et al. 2002; Sherwin 2007).

'Consumer Surplus'

Consumer surplus is derived from a measure of the area under a demand curve (Ng 1990; Mason et al. 2001; Kirkden et al. 2003; Cooper 2004). We calculated consumer surplus as the whole area under the regression between zero cost and the maximum cost an animal would pay to access each resource (Kirkden et al. 2003). To do so we calculated the area of the trapezoid ($\frac{1}{2} \times b \times (h_1 + h_2)$) created by drawing a straight line down from either end of the demand curve. In

comparing resources, a greater area indicates a higher motivation for the resource across the range of costs examined.

‘Total Expenditure’

Total expenditure is calculated as a rate of cost per unit time (Mason et al. 2001). We calculated expenditure rate by multiplying the number of visits to each compartment by the cost of access, summing across all costs and then dividing this total by the number of days in the trial. Costs were weighted using the following system: $0^\circ=1$, $22.5^\circ=2$, $45^\circ=3$, $67.5^\circ=4$ & $90^\circ=5$. Thus, for example, a mouse that climbed each incline only once would have an expenditure rate of $(1+2+3+4+5)/5 \text{ days} = 3$ and a mouse that climbed each incline 5 times would have an expenditure rate of $(5+10+15+20)/5 \text{ days} = 10$.

‘Reservation Price’

The reservation price was calculated as the maximum price each mouse was willing to pay to access the resource compartments (Mason et al. 2001). The steepest incline a mouse would climb to access each resource was recorded and means ($n=28$) were calculated to make comparisons between the resources.

Statistical Analysis

Data from the two replicate trials during experiment 1 were averaged for each mouse before statistical analysis. Data for the number and duration of visits to the resource compartments were normally distributed for four out of the five imposed costs (normal for 0° , 22.5° , 45° & 67.5°) but not normally distributed for the fifth cost (90°). We utilized a mixed linear model (Proc

Mixed) of the SAS Institute (1999) with choice as a repeated measure to test for overall effects of foraging choice, cost and their interaction on the number and duration of visits to each resource (SAS Institute 1999). Analyses conducted on both raw and ranked data yielded similar results, suggesting that valid assessment could be conducted with parametric statistics. Results from analyses on ranked data are reported. Separate analyses were conducted for the number and duration of visits to each compartment. Comparisons between foraging options were made based on differences in least-squares means, with p-values adjusted for multiple comparisons using the Tukey option.

Motivation indices were calculated for each individual and group means were derived from these individual values (n=28 for each experiment) to make comparisons between the foraging resources. Differences between means for elasticity coefficients, Y-intercepts, areas, total expenditures and reservation prices (e.g. $D1 = \text{area resource A} - \text{area resource B}$) were assessed with individual Student's t-tests (Proc Univariate, SAS Institute, 1999). All statistical calculations were two-tailed with significance level set at $\alpha=0.05$.

Results

Mice were quick to approach and interact with the foraging options immediately after being placed in the test arena. Typically, each mouse patrolled the entire apparatus, moving up and down both tubes to visit each of the foraging options before pausing to manipulate any specific resource.

Number and Duration of Visits

There was a difference in the number of visits made to the two foraging compartments (Mixed linear model: $F_{1,27}=6.51$, $P=0.017$) with mice ($n=28$) visiting the contrafreeloading compartment more frequently than the free food compartment (Tukey adjusted t test: $t_{27}=2.55$, $P=0.017$). There was an overall effect of cost on the frequency of visits made to the foraging compartments (Mixed linear model: $F_{4,108}=44.73$, $P<0.0001$) but no cost by foraging choice interaction ($F_{4,108}=0.59$, $P=0.67$). Mice persisted in visiting both compartments when faced with increasing costs between 0° and 67.5° but visited the compartments significantly less when access required a vertical (90°) climb (Tukey adjusted t test: $t_{108}\geq 6.24$, $P<0.0001$; Fig. 15).

There was a difference in the time spent in each resource compartment (Mixed linear model: $F_{1,27}=5.07$, $P=0.033$) with mice ($n=28$) tending to remain in the contrafreeloading compartment for longer durations than the free food compartment (Tukey adjusted t test: $t_{27}=2.25$, $P=0.033$; Fig. 16). Time spent in the each food compartment remained relatively stable across all costs except the 90° . Changes in time spent in both the contrafreeloading and free food compartments were affected by the cost of access (Mixed linear model: $F_{4,108}=25.16$, $P<0.0001$), but there was no cost by foraging choice interaction ($F_{4,108}=0.45$, $P=0.77$; Fig. 16).

'Price Elasticity of Demand'

The slopes of the demand functions indicate that, despite the increasing cost of gaining access, motivation remained high (i.e. demand was relatively inelastic) and equal for accessing both the contrafreeloading and the free food compartments (Table 5). There were no differences between the price elasticity coefficients of demand for free food and a contrafreeloading opportunity, as

based on the number (Student's t : $t=0.66$, $P=0.51$; Fig. 17) or duration ($t=0.04$, $P=0.97$; Fig. 18) of visits to each resource compartment.

'Intensity of Demand'

There was no difference between the intensity of demand for access to free food and the contrafreeloading opportunity (Table 5), as based on the number (Student's t : $t=1.95$, $P=0.056$) or duration ($t=1.76$, $P=0.084$) of visits to each resource compartment (Y-intercepts in Figs. 17 & 18, respectively).

'Consumer Surplus'

Consumer surplus was greater for access to a contrafreeloading opportunity than for access to free food (Table 5). The areas under the demand functions relating cost to both the number (Student's t : $t=2.26$, $P=0.027$) and duration ($t=2.51$, $P=0.015$) of visits were larger for the contrafreeloading compartment than the free food compartment. These results indicate that across the range of costs imposed during this study, mice were more highly motivated to access an opportunity to contrafreeload than free food alone.

'Total Expenditure'

There were no differences in total expenditure rates (Table 5) for gaining access to free food versus a contrafreeloading opportunity (Student's t : $t=1.22$, $P=0.23$).

‘Reservation Price’

Although mice worked to gain access to the resource compartments at all of the imposed costs used during this study, some individuals expended more effort than others. Seven of the 28 mice made a vertical climb to gain access to the free food compartment, while 11 of the 28 mice made the same climb to gain access to the contrafreeloading compartment. Averages for the maximum incline mice were willing to climb to access the two resources (Table 5) show that this difference was not significant (Student’s t: $t=0.65$, $P=0.52$).

EXPERIMENT 2: FOOD OR AN OPPORTUNITY FOR EXPLORATION—WHAT MOTIVATES MICE TO CLIMB?

In experiment 1, mice were motivated to investigate and manipulate each of the foraging items at all costs imposed. It was unclear, therefore, whether mice were attracted to food in general or to the opportunity to explore both the “free food” and “contrafreeloading opportunity.” The aim of experiment 2 was to assess the importance of food as a lure for tube climbing in mice. We thus replaced the foraging options in the two compartments with whole and empty sunflower hulls and provided a foraging opportunity outside of the compartments that required relatively no effort for exploitation. We assessed: (1) whether mice are attracted to food items specifically or whether they are attracted to the opportunity to explore resources in the foraging compartments in general and (2) whether mice are motivated to pay increasing costs to gain access food (contrafreeload) when food items can be exploited with relatively little effort.

Methods

Subjects for experiment 2 were 28 female mice (C57BL/6J) between the ages of 3 and 21 months not utilized previously and housed in the same manner as described for experiment 1. Training and testing sessions were conducted in an identical manner as outlined for experiment 1 with the following exceptions. For experiment 2, one compartment was supplied with “food” (30 whole sunflower seeds) and the other compartment contained “non-food” (empty sunflower hulls). These choices were provided in the presence of “free food” (30 sunflower kernels without hulls) located in the centre of the floor of the test arena. Whole seeds and hulled kernels were acquired from the same source, and autoclaved in the same manner, as for experiment 1. To obtain intact hulls, whole seeds were autoclaved submerged in water, which caused the hulls to become flexible and separate along the sides. Kernels were removed carefully by hand leaving behind two intact halves of the original hull. Once separated from the kernels, hull-halves were dried overnight in a 100°C drying oven. Because the dry hulls were essentially weightless, we used seed counts (30 of each type) in lieu of weights to ensure that we provided mice with similar volumes of each resource.

Mice in experiment 1 performed consistently between the two trials, so for experiment 2 a single trial (5 sessions) was conducted. In addition to recording the maximum incline each mouse was willing to climb, the number of visits and the duration of time spent in each compartment, we also recorded the number of visits and duration of time spent in contact with freely available food on the floor of the test arena. Calculation of demand and statistical analyses were conducted as outlined for experiment 1.

Results

Number and Duration of Visits

There was a difference in the number of visits made to each foraging choice (Mixed linear model: $F_{2,54}=146.32$, $P<0.0001$) with mice ($n=28$) visiting both the food (Tukey adjusted t test: $t_{54}=14.01$, $P<0.0001$) and non-food ($t_{54}=15.51$, $P<0.0001$) compartments more often than the free seeds available on the floor of the test arena. The mice visited the free seeds most on the first day of testing when no costs (0°) were imposed on accessing the resource compartments (Fig. 19a). Overall, however, visits to the free seeds were relatively infrequent (median, IQR: 1, 2 visits; Fig. 19a) and brief (Fig. 19b). There was an effect of cost on the number of visits made to the foraging resources (Mixed linear model: $F_{4,108}=21.86$, $P<0.0001$) and a foraging choice by cost interaction ($F_{8,216}=9.53$, $P<0.0001$) with mice visiting the two foraging compartments more often than the free seeds no matter what costs were imposed on accessing the compartments. There was no difference in the number of visits mice made to the food and non-food compartments (Tukey adjusted t test: $t_{54}=1.50$, $P=0.29$; Fig. 20). After an initial increase in the number of visits to both the food and non-food compartments when costs increased from 0° to 22.5° , the number of visits mice made to both compartments remained relatively steady up to a cost of 67.5° (Fig. 20). As in experiment 1, the fewest visits were made to the resource compartments when access required a vertical climb.

There was a difference in time spent with each foraging choice (Mixed linear model: $F_{2,54}=176.31$, $P<0.0001$) with mice ($n=28$) spending more time in both the food (Tukey adjusted t test: $t_{54}=14.42$, $P<0.0001$) and non-food ($t_{54}=17.63$, $P<0.0001$) compartments than they spent

interacting with the free seeds available on the floor of the test arena. Mice spent the most time interacting with the freely available seeds when the other resources were also freely available (Fig. 19b), and relatively little time (median, IQR: 0.8, 1.85 s) interacting with this resource in general (Fig. 19b). There was an effect of imposed cost (Mixed linear model: $F_{4,108}=13.64$, $P<0.0001$) on time spent with the resources and a foraging choice by cost interaction ($F_{2,216}=3.86$, $P=0.0003$). Overall, mice spent more time in the non-food than the food compartment (Tukey adjusted t test: $t_{54}=3.20$, $P=0.006$; Fig. 21).

'Price Elasticity of Demand'

Based on the slopes of the demand functions, demand was equal and relatively inelastic for the opportunity to interact with both food and non-food items (Table 5). There were no differences between the price elasticity coefficients of demand for access to food and non-food items, as based on the number (Student's t: $t=0.23$, $P=0.82$; Fig. 22) or duration ($t=0.26$, $P=0.80$; Fig. 23) of visits to each resource compartment.

'Intensity of Demand'

There were no differences in the intensity of demand for food or non-food items (Table 5). Y-intercepts were equal for both resources when considering the number (Student's t: $t=0.56$, $P=0.58$; Fig. 22) or duration ($t=1.10$, $P=0.28$; Fig. 23) of visits to the resource compartments.

‘Consumer Surplus’

Consumer surplus measures did not differ between the resources provided during experiment 2 (Table 5). The areas under the demand functions relating cost to both the number (Student’s t : $t=0.78843$, $P=0.44$) and duration ($t=1.57$, $P=0.13$) of visits to the food and non-food items were not different; indicating mice were equally motivated to access both resources.

‘Total Expenditure’

There were no differences in total expenditure rates (Table 5) for gaining access to food versus non-food ($t=0.25$, $P=0.8032$) items.

‘Reservation Price’

There was no difference in average maximum incline mice were willing to climb to access the food and non-food compartments during experiment 2 (Student’s t : $t=0.23$, $P=0.82$; Table 5). Eleven of the 28 mice made a vertical climb to gain access to the food compartment and 12 of the 28 mice made the same climb to access the non-food compartment.

DISCUSSION

In this study, we investigated contrafreeloading behaviour in laboratory mice by providing mice the opportunity to work for food items under a consumer demand paradigm. To our knowledge, this is the first study to investigate motivational strength within the context of contrafreeloading. Mice were highly motivated to investigate and manipulate each of the foraging items provided at

all costs imposed during this study, though consumption of the resources was rare, suggesting that satiation is neither an exclusive motivating factor, nor the sole endpoint, of exploratory and appetitive behaviours.

Contrafreeloading: seeking information?

Contrafreeloading may reflect an inherent motivation for animals to seek out information about the quality and accessibility of different resources (Inglis 2000; Swaisgood 2007). Animals may actively seek opportunities to learn about potential food items. Such a motivation could be evolutionarily adaptive, ensuring that an animal has the best possible information to alter its feeding behaviour in response to environmental challenges (Inglis 1983; Hughes & Duncan 1988a; Day et al. 1998; Inglis et al. 2001). Whereas this behaviour has apparent adaptive benefits in the wild, it would seem “unnecessary” in captivity when animals are provided with food ad libitum. Yet domesticated animals may retain a strong internally driven motivation (Panksepp 1998; Inglis 2000; Everitt et al. 2001; Spruijt et al., 2001) to explore and learn about environmental contingencies. We examined whether these motivational tendencies persist in laboratory mice that have been bred in captivity for thousands of generations and are generally fed ad libitum.

In our first experiment we allowed mice the opportunity to explore and manipulate two foraging options that provided different levels of information; free food and a contrafreeloading opportunity. When costs were imposed on accessing each of these resources, mice made more visits to and remained for longer durations in the contrafreeloading compartment than the free food compartment. There were no differences between the ‘price elasticity’ or ‘intensity’ of

demand for access to the free food and contrafreeloading compartments. However, the areas under the demand functions (consumer surplus) relating cost to both the number and duration of visits were larger for the contrafreeloading compartment than the free food compartment. A greater measure of consumer surplus indicates that across the range of costs imposed during this study, mice were more highly motivated to access an opportunity to contrafreeload than free food alone (Mason et al. 2001; Kirkden et al. 2003; Sherwin 2007).

This finding is not surprising when we consider the potential benefits that exploring each compartment might provide. The resources available in the free food compartment (kernels lacking hulls) could be quickly evaluated and/or consumed with minimal effort on the part of the animals. By sampling de-hulled kernels mice could gain information about the nutritional properties of sunflower seeds, but little information to build competence in resource exploitation. The second compartment set the stage for contrafreeloading by offering seeds that varied in the level of processing required before consumption. A contrafreeloading opportunity provided mice with the chance to make simultaneous (direct) comparisons between kernels with and without hulls. The contrafreeloading compartment, therefore, provided a greater opportunity for gathering information that could be useful in future foraging endeavours. Not only were mice provided with the opportunity to sample kernels to learn about the nutritional make-up of sunflower seeds, but they were also provided with the opportunity 1) to identify encapsulated food items and 2) to remove hulls, exposing the nutritious part of the seed, thereby improving their competence in future resource exploitation.

The motivation to climb tubes may have been to monitor and gather information about alternative resources in the environment (Toates 1983; Inglis & Ferguson 1986; Forkman 1996; Inglis et al. 1997, 2001) rather than a motivation to gain access to a particular food source. Contrafreeloading could be considered a form of intrinsic exploration, whereby animals engage in general exploration, rather than extrinsic exploration, which involves appetitive behaviour to meet an immediate need (Berlyne 1960). On arrival at a new food patch, contrafreeloading may thus contribute to an animal's immediate decisions about which particular bits and pieces to consume in significant amounts within a patch of apparently similar food items. Over a broader scale, in both time and space, animals could potentially diminish the risk of starvation in the future by gathering information about resources that they do not have an immediate need for but might exploit in the future.

Contrafreeloading: a tool for distinguishing food from non-food?

For wild animals facing fluctuations in food abundance in an unstable environment, intrinsic exploration may create situations in which there is an opportunity to acquire biologically useful information (Berlyne 1960; Day et al. 1998; Inglis 2000). Intrinsic exploration may facilitate the identification of new food items (Day et al. 1998) by fulfilling a motivation for animals to seek information about originally novel stimuli. Following this line of thought, contrafreeloading may not only provide a means for animals to gather information about alternative food sources (Inglis and Ferguson 1986; Forkman 1996; Inglis et al. 1997), but may serve as a behavioural mechanism for learning to distinguish food items from non food items as well.

In our second experiment, we allowed mice the choice of free seeds on the floor of the test arena as well as an opportunity to work for access to food (seeds which required de-hulling before consumption) and non-food (empty hulls which provided little to no nutrient value) items. This design created a contrafreeloading opportunity by allowing mice the option to manipulate freely available seeds or to climb through tubes to gain access to seeds that required de-hulling before consumption. Mice had the opportunity to make comparisons between kernels, kernels encapsulated within hulls and empty hulls, although work was required for accessing these resources to draw comparisons. The opportunity for simultaneous comparison of resources was therefore not provided.

Visits to the free seeds were relatively infrequent regardless of what cost was imposed on access to the other resources, and mice spent relatively little time interacting with the free seeds in general. Mice visited both resource compartments equally, but spent more time in the non-food than the food compartment. Demand was equal and relatively inelastic for the opportunity to interact with both food and non-food items. There were no differences between the ‘price elasticity,’ ‘intensity’ or ‘consumer surplus’ between the food and non-food compartments, indicating mice were equally motivated to access both resources. At first these results were somewhat surprising. We had predicted that mice would be most highly motivated to interact with whole seeds, because, as described above, kernels encapsulated within hulls provide ample information for a curious explorer. However, we may have underestimated the appeal of empty hulls.

Many animals are motivated to identify and sample the available items in their environment to assess whether they are nutritionally beneficial (Day et al. 1998). In this sense, empty hulls may have provided the greatest opportunity for information gain. Empty hulls smell like food, the exposed centres may even taste like food, but in the current experiment were not presented in the context of food (i.e. empty hulls were not presented next to de-hulled kernels). Of the three resources available to the mice during this experiment, the greatest uncertainty may have surrounded the empty hulls. A greater level of uncertainty relating to this resource could have generated more interest by the mice in terms exploration and contrafreeloading (Forkman 1996; Inglis et al. 1997, 2001). Mice may have been expressing the ultimate in anti-economic behaviour by choosing to work for the opportunity to manipulate empty hulls when free kernels were available; or alternatively, the mice may have achieved the greatest reward in terms of information gain by interacting with the most uncertain resource.

Animals don't always utilize the resources they work for

Mice were observed to paw at, pick up and mouth individual items. Careful inspection following each 10 minute testing session revealed detectable damage to some portion of each of the foraging options. Intact seeds were cracked open or noticeably chewed with the kernel sometimes removed. Kernels were broken or visibly nibbled. Hull-halves were split or broken into small bits. The mice did not, however, consume measurable quantities of any of the foraging options (as measured on a scale calibrated to detect 0.05 g changes in weight).

There are several possible explanations for this lack of consumption. 1) Mice were fed ad libitum and were only removed from their general food source (rodent pellets in the home cage)

for 10 minutes at a time for test sessions. As the subjects were not food deprived, we should not expect large quantities of food to be consumed during the test sessions. Sunflower seeds were only available to the mice during the test sessions, however, and could have been considered a ‘treat’ item worth consuming even during short bouts of exposure. 2) Mice may have been unsure of sunflower seeds as potential foraging items (novel at the beginning of training sessions) and may have been sampling small bits to ‘test’ their potential as a foraging option. This seems unlikely, though, as the mice were exposed to sunflower seeds during each training and test session. Even if mice were unsure of seeds as foraging items at the beginning of the experiment, they should have learned to recognize seeds as ‘food’ by the end of the testing sessions. It has been demonstrated that foraging and diet selection in omnivores and granivores requires considerable learning (Harrison 1985; Johnson et al. 1993; Valone & Giraldeau 1993), thus mice should have the capacity to quickly learn about new resources (Lawhon & Halfner 1981). 3) It is also possible that mice were motivated to interact with the seeds in a manner not related to consumption. Since mice were tested for only 10 minutes at a time rather than living in the apparatus continually (a “closed economy”), we did not provide any nesting material in the test apparatus. This was to allow for easy retrieval of any seeds that might be displaced by mice and to allow for easy cleaning of the apparatus between mice. Mice are known to work for access to nesting material (e.g. Roper 1975), so it is possible that we inadvertently tested motivation for a resource (nesting material) unrelated to foraging. 4) In common with many consumer demand paradigms, mice may have been willing to work for access to resources that they did not utilize. For example, in demand studies with pigs (Hutson 1988), mice (Sherwin 1996), mink (Cooper & Mason 2000) and foxes (Hovland et al. 2006) test animals will often pay high entry fees to get access to resources without interacting with them. In our experiments, mice interacted with all of

the foraging items, possibly more related to exploratory or appetitive behaviours than consummatory behaviour.

Demand: equally strong or non existent?

In considering our measures of demand for access to the resources utilized throughout this study (Table 1), it appears that mice were highly motivated to access all of the resource compartments. Similar findings are reported in other studies that utilize a consumer demand approach with mice (Sherwin 1998, 2003, 2004; Sherwin & Nicol 1995; Sherwin & Nicol 1996) indicating that mice are highly motivated to patrol new areas that are made accessible to them. A strong motivation to explore in general may contribute to the willingness of mice to work for access to resource compartments. However, the fact that we found significant differences in the number and/or duration of visits mice made to each individual resource compartment indicates that it is unlikely mice were visiting resources randomly (Sherwin 1996).

The literature indicates that C57BL/6 mice readily acquire spatial discrimination tasks whether it is learning the location of nose holes in an operant chamber (Delcasso et al. 2007), platform location in a Morris water maze (Paylor et al. 1993; Fordyce et al. 1995; Stavnezer et al. 2002) or resource location in a radial maze (Ammassari-Teule et al. 1993) and demonstrate greater ability at these tasks than other strains of mice (Ammassari-Teule et al. 1993; Paylor et al. 1993; Fordyce et al. 1995; Mihalick et al. 2000; Brooks et al. 2005). We are, therefore, fairly confident that the mice were capable of learning the location of the foraging options provided in our experiments.

Demand indices in experiment 2 were generally higher than in experiment 1 (Table 1). It is unlikely that this disparity can be attributed solely to group differences between the mice used in the two experiments given that the mice from both experiments were of the same strain, breeding stock and relative ages and were housed in the same room in an identical manner. It is possible that having access to three different sources of materials (kernels, whole seeds and empty hulls) stimulates a stronger motivation to explore than when only two resources are available (kernels, whole seeds). The lack of opportunity for direct comparison between resources may have also contributed to the increase in work output by mice in experiment 2, as comparisons between resources were not possible unless mice worked for each individual resource separately.

The consumer demand approach

Although the use of a consumer demand approach for assessing animal motivation is not a new concept (Lea 1978; Hursh 1980; Dawkins 1983), careful evaluation of the associated methods is an ongoing process. Techniques continue to evolve as psychologists, applied ethologists and animal welfare scientists alike attempt to identify the most objective means for assessing animal motivation (Kirkden et al. 2003; Warburton & Mason 2003; Cooper 2004; Kirkden & Pajor 2006). It has been suggested (e.g. Cooper 2004) that where possible naturalistic tasks should be used to impose costs on animals, as these tasks require little training and are less prone to operant bias than many trained laboratory tasks (e.g. lever pressing). We designed an apparatus incorporating this naturalistic approach which proved effective in assessing the motivation of mice to a variety of foraging resources. As part of their natural foraging repertoire, mice readily climb up branches or into plants to exploit seed patches. Though these activities are far removed

from those typical of domesticated mice in a laboratory setting, mice demonstrated great ability at climbing through tubes and a willingness to do so to access resource compartments. The knowledge gained in this experiment can be used to investigate further the motivation of mice for a wide variety of resources.

Strength of motivation can be used to assess the importance of activities or resources that might improve captive housing conditions because motivation is inherently linked to feelings of pleasure and aversion (Cabanac 1979; Warburton and Mason 2003). Animals may suffer if they are strongly motivated to perform certain activities that their captive surroundings do not permit (Dawkins 1988, 1990). Thus, providing resources that allow animals to carry out favoured activities is suggested to improve quality of life in captivity (Dawkins 1990; Cooper and Mason 2000). If the motivation to seek information in the environment is intrinsically regulated then housing mice in an environment that does not provide opportunities for exploration and information gain may lead to various negative emotional consequences and abnormal behaviours (Clubb & Mason 2003). Recent evidence suggests that standard housing of laboratory rodents may impose constraints on brain and behavioural development that could compromise the utility of rodents for biomedical and behavioural research (e.g. Wurbel 2001). A better understanding of contrafreeloading behaviour may offer a biological basis for refinement through foraging enrichment. Our ability to develop captive environments which promote the welfare of laboratory rodents is dependent upon knowledge of which aspects of the environment are important to the animals. Tests of animal motivation can be a useful tool in the pursuit of this goal. Our results indicate that laboratory mice are still motivated to perform many of the same exploratory activities as their wild counterparts. Contrafreeloading is not 'luxury' behaviour

performed only when food choices are easily accessible, but rather a behavioural opportunity that mice may actively seek.

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Table 5. Summary of results for consumer demand measures. Mean (\pm SE) for ‘Price Elasticity,’ ‘Motivation Intensity,’ ‘Consumer Surplus,’ ‘Total Expenditure’ & ‘Maximum Price Paid.’

Resource	Measure V=visits D=duration	‘Price Elasticity’ (Slope)	‘Motivation Intensity’ (Y-Intercept)	‘Consumer Surplus’ (Area)	‘Total Expenditure’ (Rate)	‘Maximum Price’ (Angle)
Experiment 1						
“Contrafreeloading” (Whole seeds + hulled kernels)	V	-0.18 \pm 0.02	1.03 \pm 0.02	1.66 \pm 0.04	18.5 \pm 1.29	73.53 \pm 1.67
	D	-0.30 \pm 0.04	1.96 \pm 0.04	3.25 \pm 0.09		
“Free Food” (Hulled kernels)	V	-0.16 \pm 0.02	0.95 \pm 0.03	1.54 \pm 0.06	16.8 \pm 1.28	72.32 \pm 1.69
	D	-0.30 \pm 0.04	1.82 \pm 0.07	2.99 \pm 0.11		
Experiment 2						
“Food” (Whole seeds)	V	-0.04 \pm 0.04	0.84 \pm 0.06	1.56 \pm 0.06	19.56 \pm 1.44	76.34 \pm 2.11
	D	-0.09 \pm 0.09	1.78 \pm 0.12	3.34 \pm 0.11		
“Non-Food” (Empty hulls)	V	-0.06 \pm 0.03	0.89 \pm 0.05	1.64 \pm 0.06	20.15 \pm 1.26	77.14 \pm 2.14
	D	-0.12 \pm 0.07	1.96 \pm 0.10	3.61 \pm 0.13		

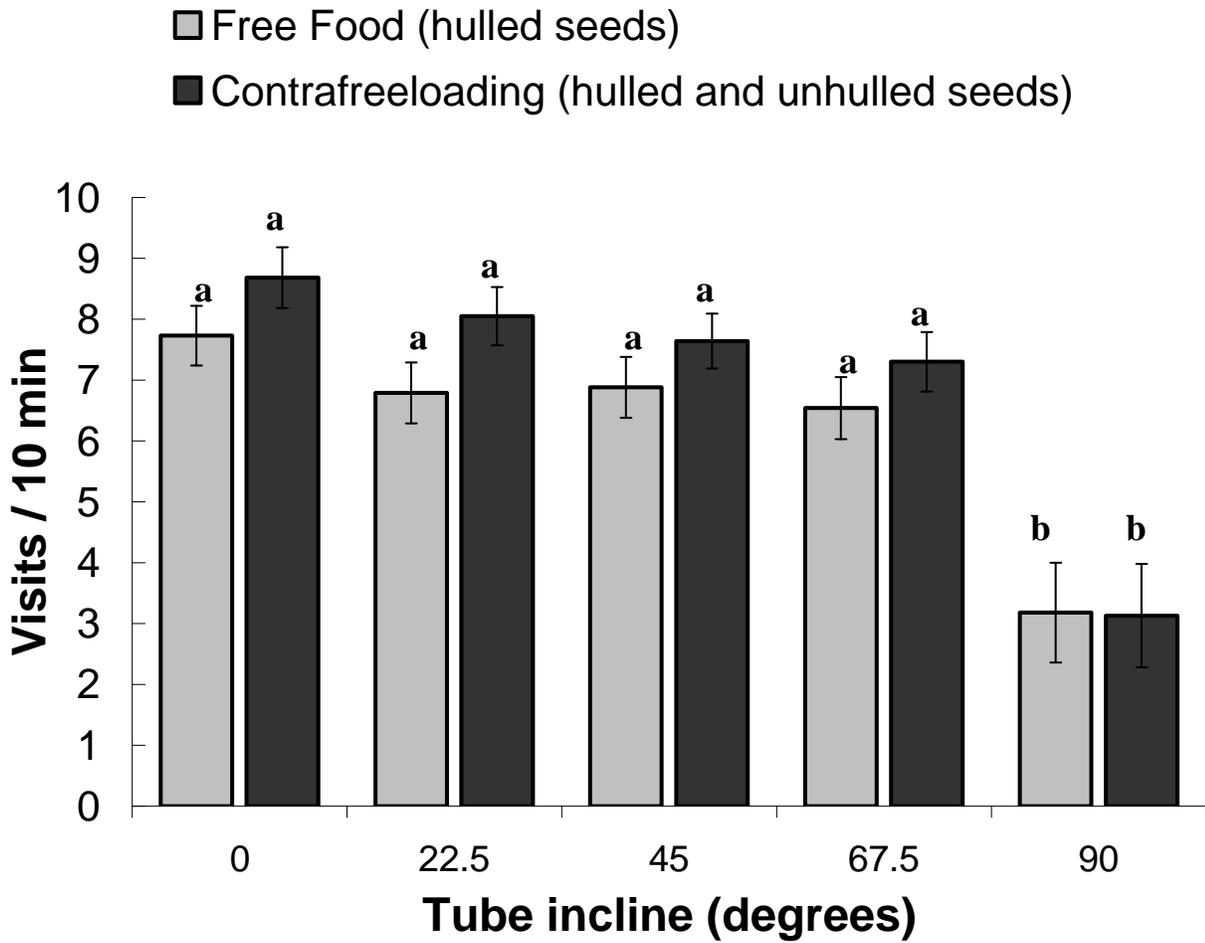


Figure 15. Mean (\pm SE) number of visits by mice ($n=28$) to the resource compartments as a function of the cost of access (incline of tube leading to compartment). Letters indicate differences across foraging options and costs ($P<0.05$).

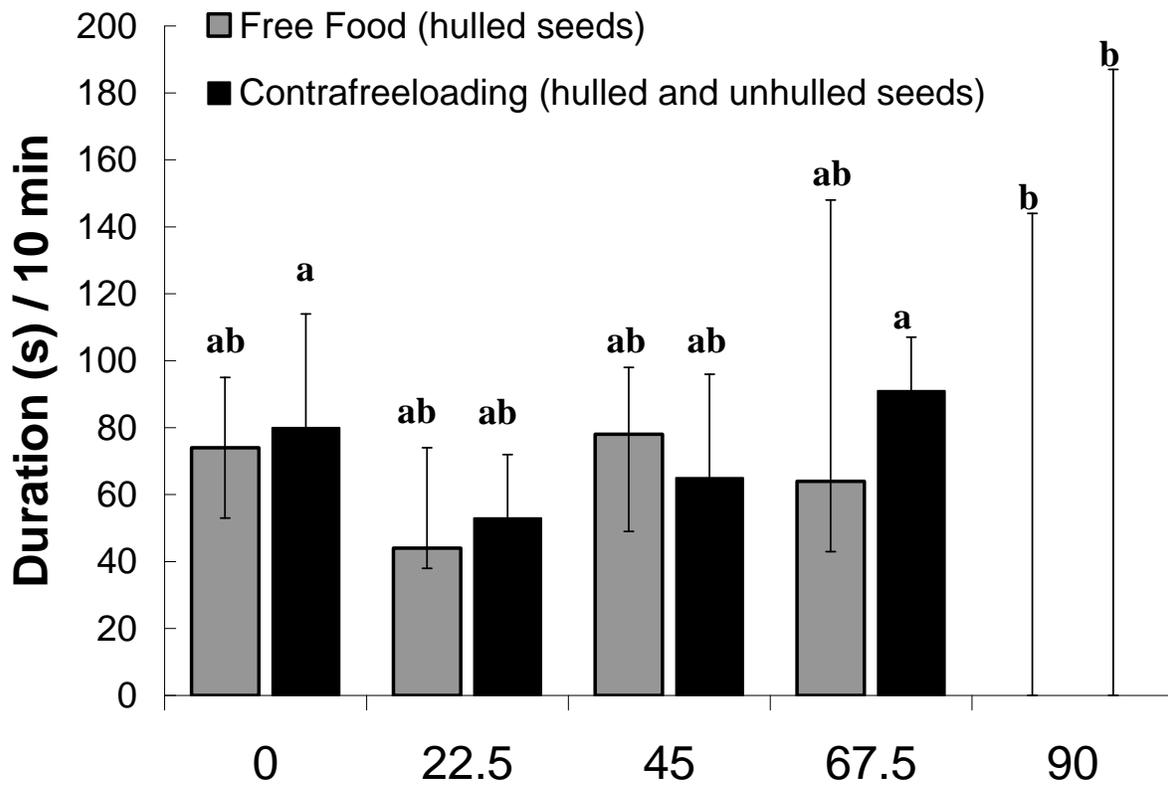


Figure 16. Median (IQR) time mice (n=28) spent in each resource compartment as a function of the cost of access (incline of tube leading to compartment). Letters indicate differences across foraging options and costs (P<0.05).

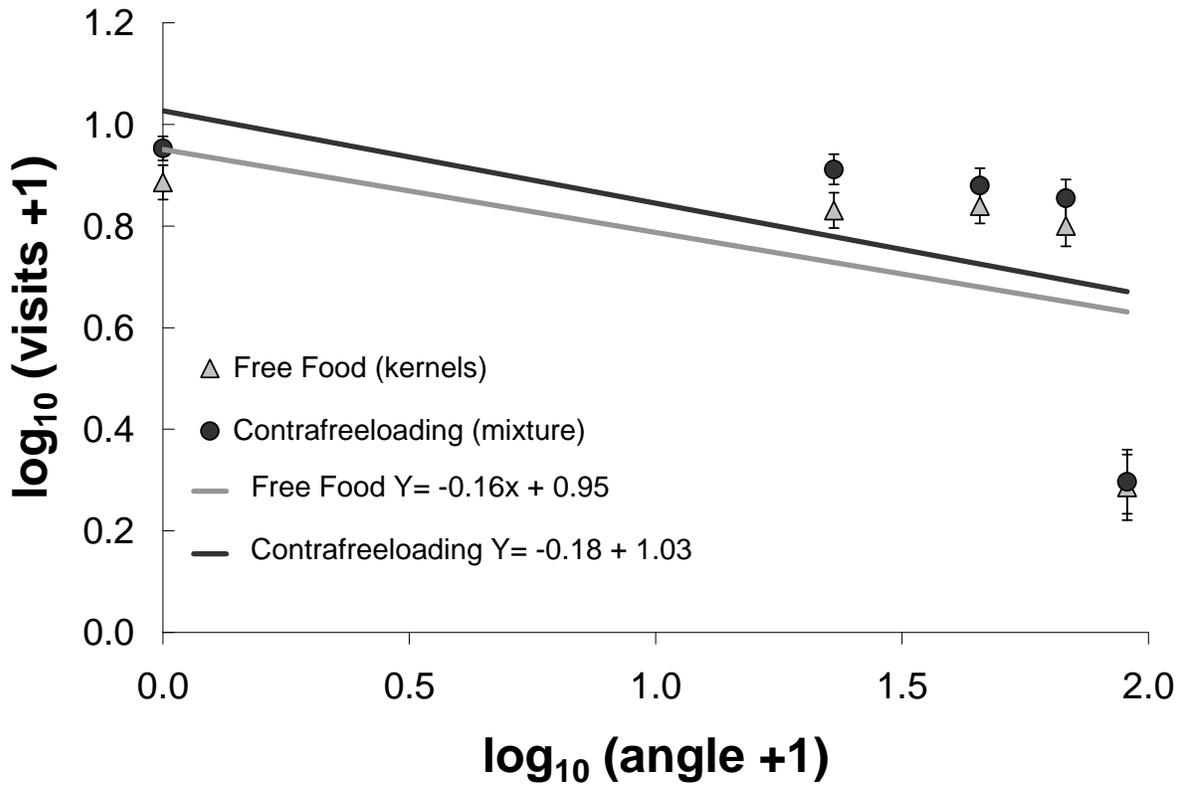


Figure 17. Mean (\pm SE) number of visits by mice ($n=28$) to the resource compartments as a demand function of the cost of access (log-log scale). Slope of regression lines indicates ‘elasticity of demand’ and Y-intercept indicates ‘intensity of demand.’

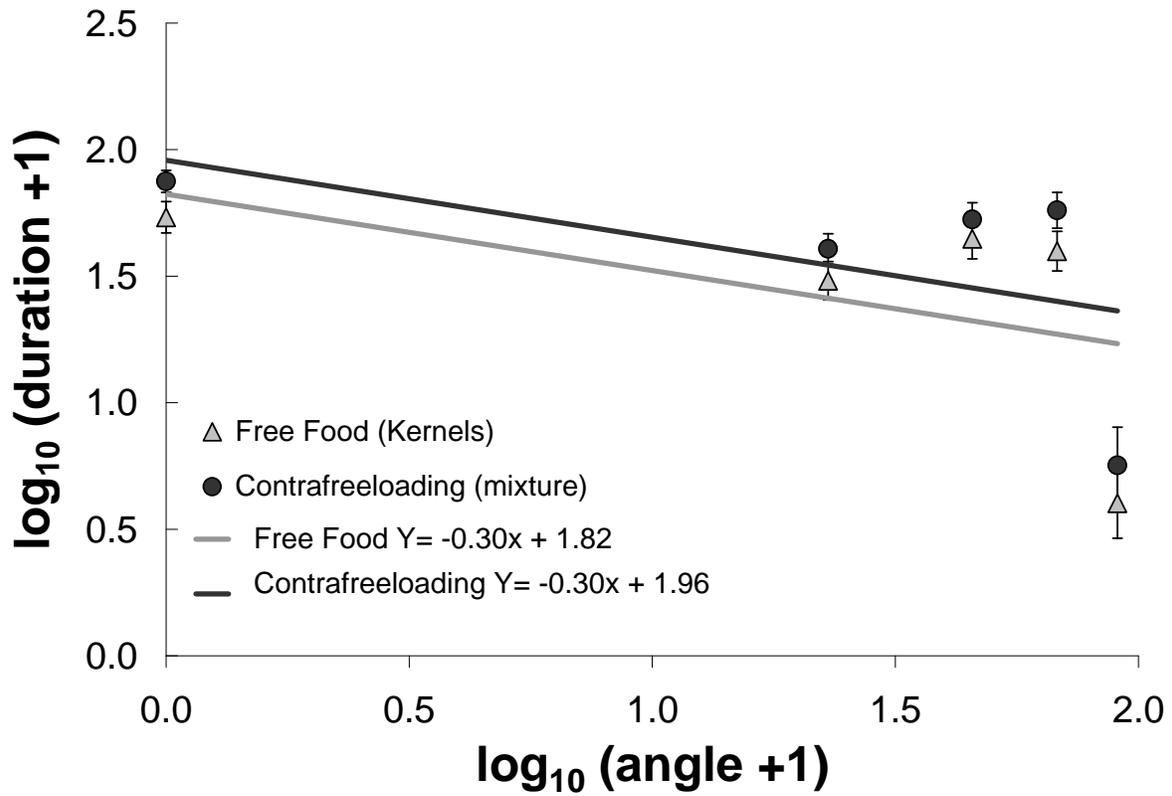


Figure 18. Mean (\pm SE) time mice ($n=28$) spent in each resource compartment as a demand function of the cost of access (log-log scale). Slope of regression lines indicates ‘elasticity of demand’ and Y-intercept indicates ‘intensity of demand.’

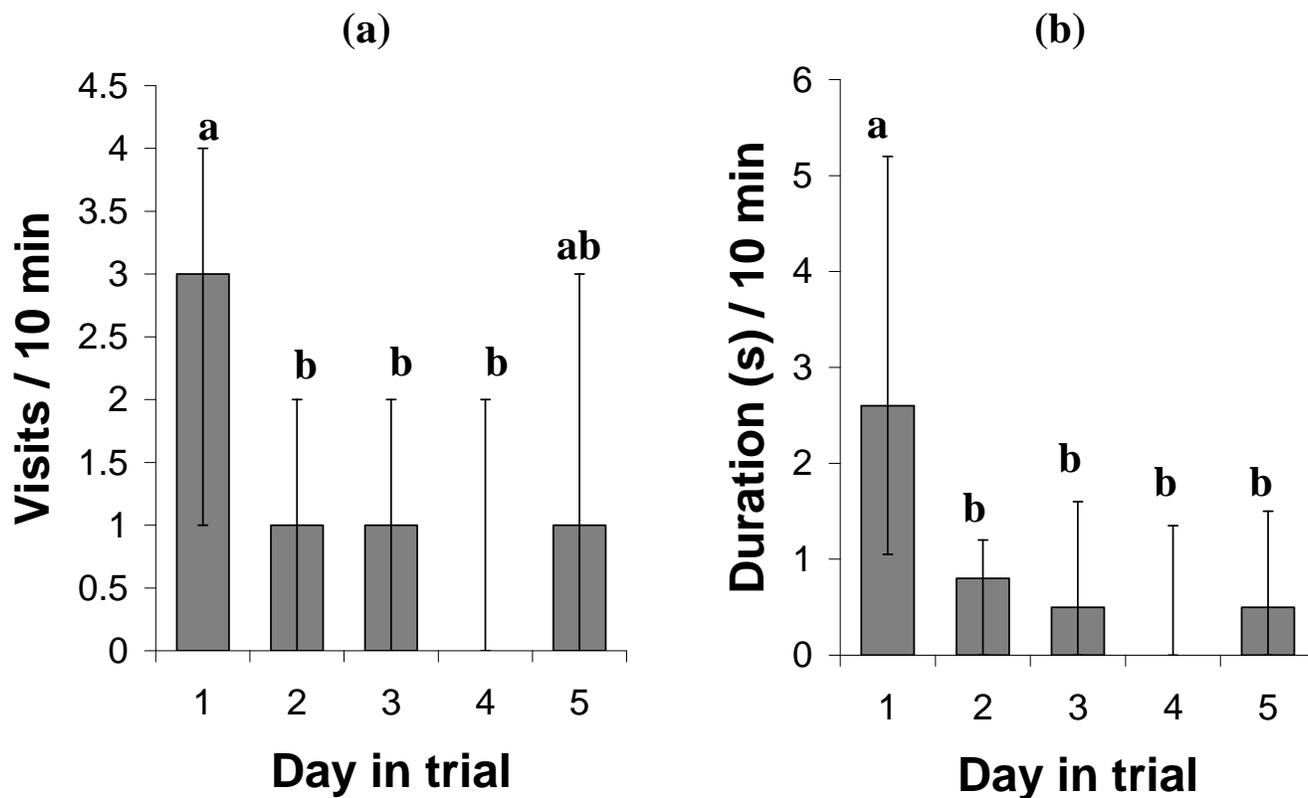


Figure 19. Median (\pm Q1, Q3) for (A) number and (B) duration of visits by mice (n=28) to freely available hulled sunflower kernels on the floor of the test arena. Letters indicate differences between days in trial ($P < 0.05$).

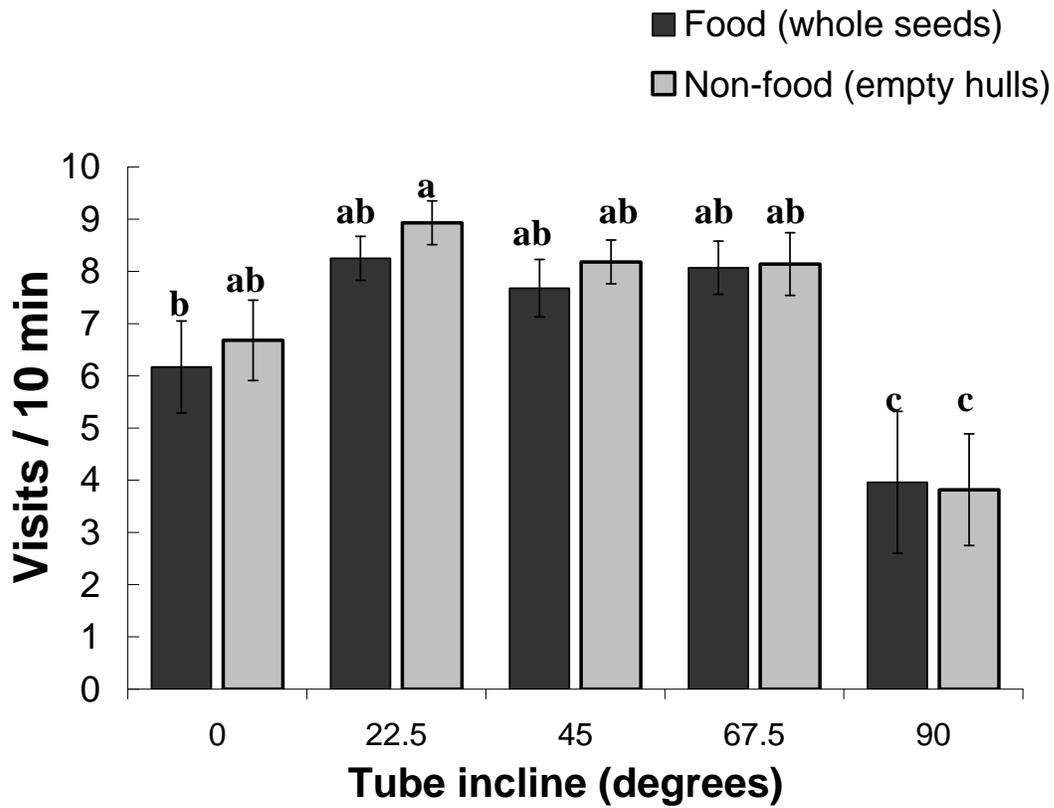


Figure 20. Mean (\pm SE) number of visits by mice ($n=28$) to the resource compartments as a function of the cost of access (incline of tube leading to compartment). Letters indicate differences across foraging options and costs ($P<0.05$).

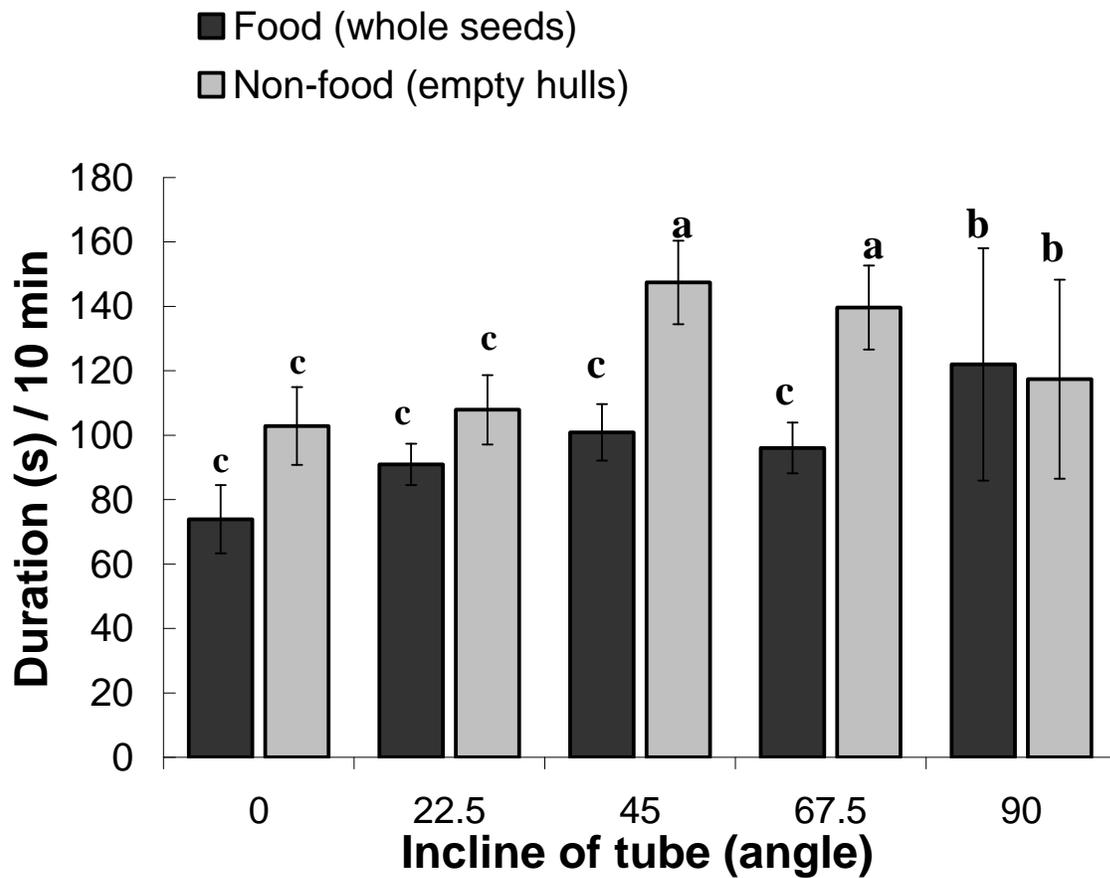


Figure 21. Mean (\pm SE) time mice ($n=28$) spent in each resource compartment as a function of the cost of access (incline of tube leading to compartment). Letters indicate differences across foraging items and costs ($P < 0.05$).

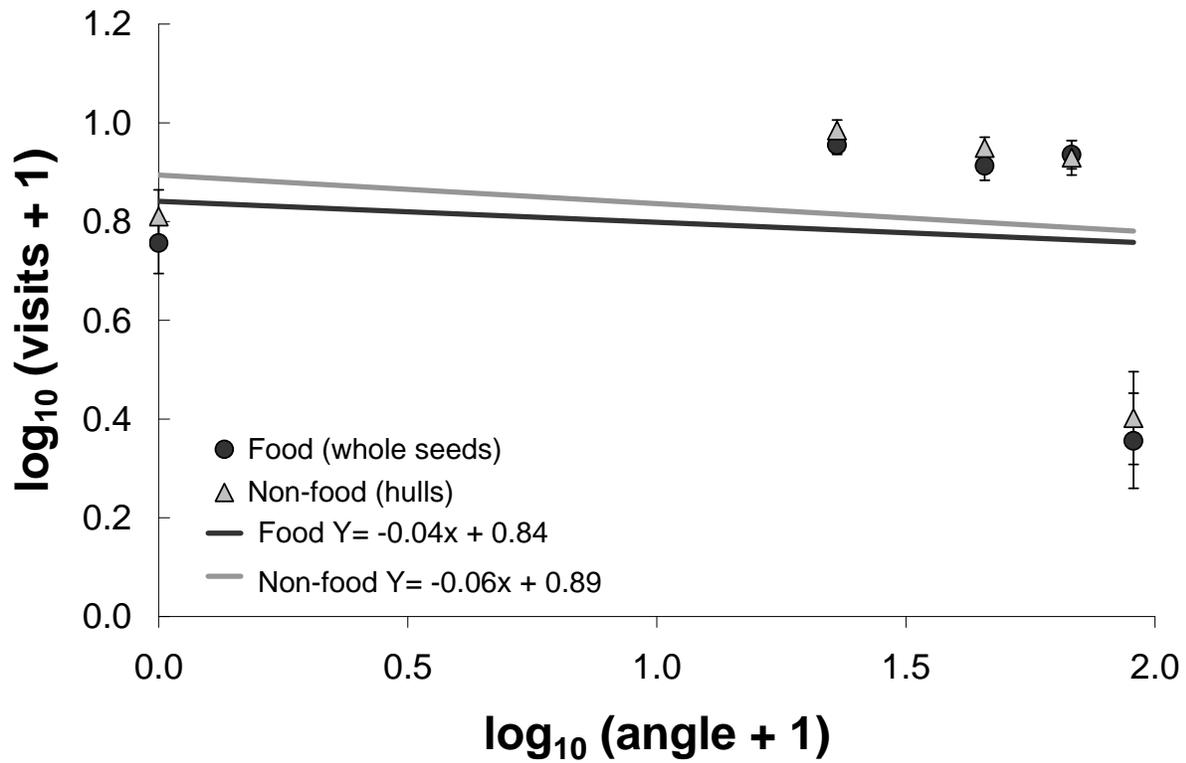


Figure 22. Mean (\pm SE) number of visits by mice ($n=28$) to the resource compartments as a demand function of the cost of access (log-log scale). Slope of regression lines indicates ‘elasticity of demand’ and Y-intercept indicates ‘intensity of demand.’

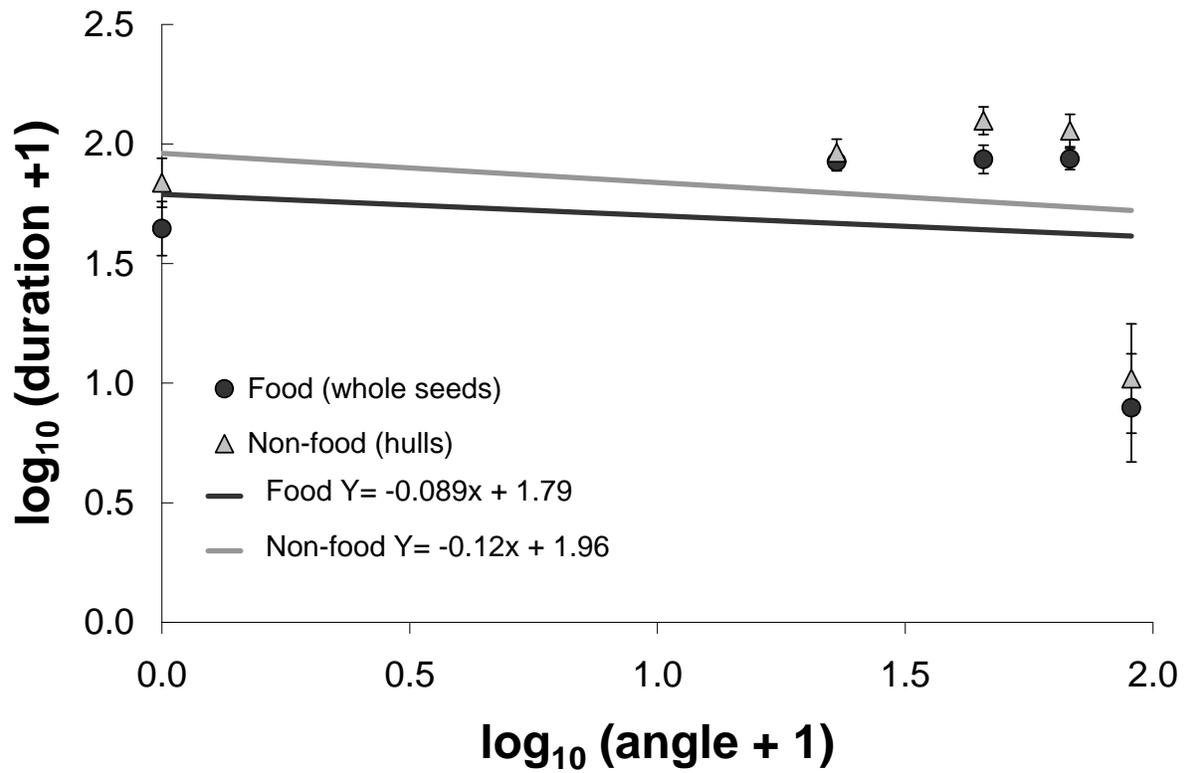


Figure 23. Mean (\pm SE) time mice ($n=28$) spent in each resource compartment as a demand function of the cost of access (log-log scale). Slope of regression lines indicates ‘elasticity of demand’ and Y-intercept indicates ‘intensity of demand.’

CHAPTER FIVE

GENERAL DISCUSSION

I am interested in utilizing environmental enrichment to improve the welfare of captive animals. This includes identifying the behavioral opportunities that are sought by animals in captivity and providing stimuli to fulfill these motivations. A more complete understanding of behavior that departs from optimality and the mechanisms underlying animal foraging decisions is useful for the design of salient foraging enrichment. I have a particular interest in the development of foraging enrichments based on an improved understanding of the phenomenon of contrafreeloading, a topic that is interesting from both basic and applied perspectives.

My studies of contrafreeloading behavior in three captive species demonstrate that, when housed in captivity with access to reliable, easily exploited food sources, animals may retain a seeking motivation that is likely adaptive under natural conditions, where survival and reproduction are dependent upon finding resources in an unpredictable environment. The studies described in the previous chapters contribute new information to the literature on contrafreeloading and provide new insights for addressing housing standards for animals in zoological, production and research settings. My findings also have potential relevance to conservation of endangered species. Animals in conservation programs must acquire skills for food harvesting before reintroduction into the wild. The provision of contrafreeloading opportunities in pre-release captive environments may create the opportunity for learning the food harvesting contingencies necessary for survival. Contrafreeloading studies also have implications for advancing our basic understanding of the role of cognition and motivation in

foraging behavior. Improved understanding of these systems will help to advance foraging theory by enhancing the predictive value of models of foraging behavior.

Given time and resources, I would extend each of my studies to delve deeper into the motivations underlying contrafreeloading. While my studies were successful in highlighting aspects of contrafreeloading that are relevant to the design of foraging enrichment for captive animals, there are still many questions that remain to be answered. In this chapter I will discuss the limitations of each of my studies and propose future directions for research relating to unraveling the behavioral mechanisms behind contrafreeloading.

Contrafreeloading in grizzly bears

The two experiments I conducted with grizzly bears were designed to assess information primacy as a possible theoretical foundation for foraging enrichment under captive conditions. While these experiments revealed new information regarding the effects of food restriction and effort on contrafreeloading in grizzly bears (a species never before investigated in the context of contrafreeloading), the design did not allow for a definitive test as to whether contrafreeloading results in information gain. My studies demonstrate that bears do contrafreeload but not why bears contrafreeload. There are presently five published studies that test information primacy as the motivating factor behind contrafreeloading (Inglis & Ferguson 1986; Forkman 1991, 1996; Bean et al. 1999; Lindqvist et al. 2002) and only two studies that test for information gain by the animal subjects (Bean et al. 1999; Lindqvist et al. 2002), a clear indication of the difficulty in addressing this problem.

Several questions are of importance. First, do bears gain information by manipulating concealed food items? Second, does contrafreeloading facilitate information gain or can the same information be gained simply by working for food? Third, how can we assess whether this information is recalled and used in future foraging endeavors?

Do bears gain information by manipulating concealed food items?

In an extensive review of the contrafreeloading literature, Inglis and colleagues (1997, 2001) demonstrated that most contrafreeloading studies fit within the predictions of a ‘fuzzy model’ for information primacy. As reviewed in chapter 1, this model predicts a negative relationship between level of hunger and contrafreeloading, with satiated animals engaging in the most contrafreeloading; a negative relationship between high levels of effort needed to exploit earned food and contrafreeloading; and an inverted-u relationship between levels of uncertainty (i.e. novelty, ambiguity or unpredictability) surrounding earned food and contrafreeloading. Despite some variability (including my own experiment where highly restricted bears contrafreeload) the majority of published contrafreeloading accounts can be explained by these predictions. These trends, however, do not necessarily provide evidence that contrafreeloading serves to allow animals to gather information.

Experimental support for information gain during bouts of contrafreeloading has come from two studies with captive and domestic birds (Bean et al. 1999; Lindqvist et al. 2002) that tested whether animals use information gained during contrafreeloading bouts to make

subsequent foraging decisions. The authors predicted that if birds are allowed to contrafreeload at foraging patches of different food quantities, then they should learn the location and contents of each patch and use this information in later ‘knowledge tests.’ In both studies, birds were food deprived and tested in extinction with the best patch removed and reliably chose the second best patch on first approach, suggesting that the birds could indeed recall information relating to the quality and location of the food items (Bean et al. 1999; Lindqvist et al. 2002). This paradigm could be replicated with bears allowing individuals to contrafreeload at foraging patches that differ in the quantity of food available (e.g. boxes with varying quantities of apples concealed within) to assess whether bears are capable of recalling the location of the most valuable patches. I predict that bears are capable of such tasks and most likely perform similar feats during their natural foraging behavior. Such ‘knowledge tests,’ however, would not provide definitive evidence that contrafreeloading is an important source of information gain. Animals may acquire information about foraging patches simply by working for or sampling from food patches regardless of whether they are exposed to a contrafreeloading paradigm.

Wild animals are capable of gaining information about foraging patches through exploration even when free food is not abundantly available. Though there are anecdotal accounts of contrafreeloading by wild animals (e.g. bears continuing to fish for salmon during spawning season when moribund salmon can be easily obtained along the river bank), field studies of contrafreeloading are absent from the literature, suggesting that the contrafreeloading paradigm is difficult to control experimentally in a natural environment. Bears are highly intelligent, curious animals that have a large capacity for learning. These adaptations help grizzlies exploit a wide variety of seasonal food resources over expansive home ranges

(Hilderbrand et al. 1999; Rode & Robbins 2000). Grizzly bears are efficient fishers, terrestrial scavengers and predators (Mattson 1997), and will consume leaves, roots and fruits from an extensive assortment of plant species (Rode et al. 2001). For the grizzly bear, survival is dependent upon the ability to locate and exploit variable food patches; this dependence is paired with a need for the capacity to learn about the location, quality and accessibility of alternative food patches. Thus, bears must have an inherent mechanism for acquiring information about their environments. It is the burden of the researcher to tease out the role of contrafreeloading in this information acquisition.

Does contrafreeloading facilitate information gain?

To fully understand the function of contrafreeloading it will be necessary to identify the specific value contrafreeloading opportunities contribute to information gain. In other words, we must find a way to separate the exclusive attributes of a contrafreeloading opportunity that differ from those provided by working for food alone. If contrafreeloading facilitates information gain, then, plausibly, an animal that demonstrates minimal contrafreeloading should obtain less information than an animal that demonstrates maximal contrafreeloading. There are limitations, of course, as there will be a cap on the amount of information that can be gained from any specific resource. There is some experimental support for this hypothesis. As described in chapter 1, Coburn & Tarte (1976) observed that rats who expressed very low levels of contrafreeloading in an operant chamber were unable to immediately recall the lever pressing response when the free food option was removed from the chamber requiring animals to work for food. Conversely, rats that had demonstrated very high levels of contrafreeloading continued to lever press and maintained their intake levels after free food removal. Though this study was designed to examine rearing effects

on contrafreeloading, and not information primacy per se, these results support the notion that contrafreeloading facilitates information gain.

Bean and colleagues (1999) used food deprivation to vary the level of contrafreeloading expressed by starlings to test whether reduced contrafreeloading would result in limited information gain. Reductions in contrafreeloading behavior did not produce apparent reductions in learned information (Bean et al. 1999). By contrast, Lindqvist and colleagues (2002) provided evidence suggesting that lower contrafreeloading by domestic fowl than jungle fowl was associated with reduced information gain by the domestic fowl. They recognized, however, that this finding could be based solely on a breed difference in learning capabilities. Further examination of the level of information gained relative to the level of contrafreeloading performed is necessary to resolve conflicts within the literature.

To investigate the role of contrafreeloading in information gain it would be useful to limit contrafreeloading experience between groups of animals and compare their foraging responses in subsequent foraging tasks. Previous studies examining contrafreeloading in relation to information gain have not assessed the information that can be gleaned when free food is not provided. I might subject three groups of bears to different foraging treatments: 1) free apples in a pile and a large bin filled with soil; 2) free apples in a pile and a large bin with apples hidden under soil; and 3) a large bin with apples hidden under soil, and a pile of soil. I would allow individuals to explore these items in their home pens for 30 minutes per day for three consecutive days. Some months later, I would subject each bear to a 'knowledge test' where I would provide one bin identical to those provided in the treatment period with apples hidden in

soil to food deprived bears. I would then compare responses between treatment groups by looking at the latency of approach to the bin, the latency to extraction of apples from the bin and efficiency in food consumption over a 30 minute period. If contrafreeloading facilitates information gain, then bears that were subject to treatment 2 should demonstrate better proficiency at food extraction than bears subject to treatments 1 and 3. If working for food provides equivalent levels of information regardless of the presence of free food, then I would expect no differences between treatments 2 and 3. If the task of extracting apples can be learned quickly I would expect no differences between the three treatments.

Contrafreeloading may facilitate information gain if having a choice between free food and earned food is beneficial. Presenting free and earned food simultaneously may allow animals to make comparisons and draw inferences from the two options. For example, a squirrel that is provided with a whole walnut and a walnut without a shell may learn to associate whole walnuts with the nutritious components that lie within. Alternatively, providing an animal with a choice between free and earned food introduces an element of environmental control. In this regard, even if choice does not facilitate information gain, it may be important because it provides an opportunity for an animal to take control over its environment. Animals find the ability to influence their environment rewarding (e.g. Markowitz & Line 1991; Hagen & Broom 2004) and loss of environmental control may even increase stress (Overmier et al. 1980). It is well documented that a perceived lack of control may inhibit learning (see Seligman 1975 for a review). Most captive animals are provided with little control over their environment. Human caretakers provide basic necessities (e.g. food, water, clean bedding) on a regular and predictable schedule, offering the captive inhabitant little control over its environment. Following this line of

thought, contrafreeloading may facilitate learning by providing animals with an element of control (i.e. the choice of how and from where to forage). Contrafreeloading, therefore, would serve as an important mechanism for information gain in captive animals.

Is information gained through contrafreeloading stored and used in the future?

There is a lack of evidence in the literature to support the idea that contrafreeloading is actually a beneficial means for gathering information about alternative resources that could be exploited in the future if more readily accessible food is unavailable. Coburn & Tarte (1976) observed rats to demonstrate knowledge gained through contrafreeloading immediately following the completion of contrafreeloading trials. Similarly, previous researchers who have incorporated ‘knowledge tests’ to assess information gain through contrafreeloading have conducted these tests on the day immediately following contrafreeloading sessions (Bean et al. 1999; Lindqvist et al. 2002).

Evidence to support the assumption that animals gather information for use when reliable resources become depleted will come from tests that require knowledge recollection in situations with separation from the contrafreeloading paradigm. For example, referring to the study I outlined to test knowledge acquisition in bears in the previous section, we could provide bins with apples hidden in soil to bears in an area outside of their home pen several days or weeks after initial exposure. It would be interesting to compare bears from treatments 1-3 outlined above to see if there were any lasting effects of differential exposure to the foraging resources. If choice facilitates learning in a contrafreeloading paradigm, then we may see evidence that animals from treatment 2 retain more information than animals from the other two treatments.

‘Knowledge tests’ conducted immediately following exposure to foraging resources may test short term memory, but long term memories may be more useful for an animal foraging in an unpredictable environment. Though information primacy predicts that preference will be given to information that has been recently updated (Inglis 1983; Inglis 2000), in a situation where recent information is not useful in finding a solution for a problem, the ability to draw upon past events will be adaptive.

Applications for enriching captive bear habitats

The fact that bears have a naturally wide-ranging, far-traveling lifestyle makes them among the most difficult animals to keep in captivity (Clubb & Mason 2007). Bears spend a large portion of their time in the wild foraging, by tearing apart rotting trees and logs, harvesting seasonal fruits, uprooting tubers, digging into the dens of small mammals, fishing and scavenging (Forthman et al. 1992; Hilderbrand et al. 1999; Mattson 1997; Rode et al. 2001; Rode & Robbins 2000). These types of habitat-disruptive activities, though functioning to stimulate exploratory behavior, make it difficult and costly to maintain bears in captive environments with natural substrates and vegetation (Forthman et al. 1992). For these reasons, many captive bears find themselves in artificial enclosures lacking in complexity.

Frustration of seeking motivation in captive carnivores may lead to its expression in undesirable forms such as stereotyped pacing (Clubb & Mason 2003). It is, therefore, important to provide behavioral opportunities that satisfy seeking motivation. The ‘missing variables’ in captive bear habitats may be the stimuli and the challenges that are encountered when moving across large ranges in the wild (Clubb & Mason 2007). These may include the cognitive

challenges faced when making decisions in a variable environment (Meehan & Mench 2007), especially for an animal whose natural foraging behavior requires repeated exploitation of patchily distributed resources. The ability to exert some level of control over the environment may be especially important for wide-ranging carnivores (Morgan & Tromborg 2007). Wild bears make a multitude of daily choices, as they seek out desired resources. Thwarting opportunities for control may, therefore, be very stressful (Clubb & Mason 2007).

Provision of contrafreeloading opportunities for captive bears could provide opportunities for exploration, cognitive challenge, a means to provide nutrients and an element of control. If bears are motivated to contrafreeload as a means to explore and gather information about the resources provided, then the effectiveness of this opportunity as enrichment may be short lived. If the means by which animals are made to work for food and the food items themselves are varied, interest may be maintained over time. There will always be an upper limit to the amount of information that can be gained from a specific foraging opportunity. Animals, however, will continually check features in their home range for changes (Inglis et al. 1997), so rotation of foraging items within the same device or the introduction of new devices will provide opportunities for new knowledge acquisition (Gifford et al. 2007; Meehan & Mench 2007).

Contrafreeloading in chickens

The three studies I conducted with chickens were designed to assess the potential implications contrafreeloading may have for the design of foraging enrichment programs aimed at reducing behavioral problems such as cannibalism and feather pecking. While these experiments provided new insight into the variability of contrafreeloading behavior between groups of birds, they did

not provide evidence for definitive connections between differences in foraging strategies and cannibalistic tendencies between the sexes. There are many questions that remain to be answered relating to the possible mechanisms that underlie these behaviors in domestic fowl.

Blokhuis (1986) suggested that feather pecking and cannibalism may be related to foraging behavior. He hypothesized that redirection of ground pecking takes place because of a low incentive value of housing systems without proper foraging substrate. Birds that perform more foraging behavior, and less resting and dust bathing, when young may be more likely to perform severe feather pecking as adults (Newberry et al. in press). Several authors have stressed the close resemblance of feather pecking and cannibalism to foraging behavior (Martin 1987; Blokhuis 1986; Huber-Eicher & Wechsler 1997). These ideas have led to the development of a foraging hypothesis for cannibalistic behavior in which feather pecking and cannibalism are thought to represent foraging behavior that becomes redirected towards conspecifics in the absence of more appropriate pecking stimuli within the captive environment (Huber-Eicher & Wechsler 1997; Cloutier et al. 2002). Cannibalistic behavior in domestic fowl may reflect stimulation of the seeking system in hens. If this is the case, then provision of behavioral opportunities to fulfill this seeking motivation may reduce cannibalistic behavior.

Several questions are of importance. Are hens strongly motivated to perform contrafreeloading behavior? Do hens that contrafreeload also perform cannibalistic acts? Can we use contrafreeloading as a predictor for cannibalistic behavior? Can contrafreeloading act as a substitute for cannibalistic behavior?

Are hens strongly motivated to perform contrafreeloading behavior?

Contrafreeloading has been reported in both jungle fowl and domestic fowl (Schütz & Jensen 2001; Lindqvist et al. 2002; Lindqvist et al. 2006). Hens will reliably explore and exploit sub-optimal foraging resources when more readily available foraging resources are present, however little is known about the motivation in relation to contrafreeloading in chickens. Given the possible relationship between restricted foraging behavior and the development of feather pecking and cannibalism in laying hens, a motivation towards contrafreeloading may provide insights into the motivational system underlying cannibalism. This is important from an animal welfare perspective because a better understanding of the motivational system underlying cannibalistic behavior is needed to facilitate its prevention without resorting to beak trimming.

A consumer demand approach could be utilized to test the hypothesis that laying hens are motivated to contrafreeload. Pilot studies suggest that laying hens will readily tug at string, bunched feathers, synthetic worms and straw. I would incorporate this element of natural feeding behavior into a consumer demand task where hens are required to work for access to foraging compartments. Hens could be presented with the choice to work for compartments containing one of four options: 1) free food only, 2) a contrafreeloading opportunity (the same food as in the free food compartment, available in both free and earned form), 3) earned food only, and 4) an empty compartment as a control for the attractiveness of the extra space or the consumer demand task alone. Hens would be required to tug at string which in turn would release a door providing access to the foraging compartments. The cost for accessing the compartments would be manipulated by increasing the force of tug on the string required to access the compartments. I predict that (1) laying hens will work for the opportunity to

contrafreeload and (2) laying hens will pay a higher cost for the opportunity to contrafreeload than to access free food alone, earned food alone, or an empty compartment.

A strong motivation to contrafreeload in hens may reflect a motivation to explore and seek information about the environment. If hens possess a strong seeking motivation that is thwarted by a captive environment that does not allow its performance, they may develop unwanted or compulsive behaviors (Garner 2005). Barbering in laboratory mice and psychogenic feather picking in parrots have been described as compulsive behaviors (Garner 2005) that arise from inadequacies in the captive environment. If severe or stereotyped feather pecking could be classified along the same lines, there may be a relationship between the development of these behaviors and inadequacies in the environment.

Are contrafreeloaders also cannibals?

If contrafreeloading is a reflection of a strong motivation to explore and gather information about the environment (Inglis 2000; Jones & Pillay 2004), and compulsive behaviors are a reflection of thwarted seeking motivation due to inadequacies in the environment (Garner 2005), there may be a link between contrafreeloading and cannibalism if these two behaviors both relate to seeking motivation. This hypothesis could be tested by examining whether any correlation exists between contrafreeloading and cannibalism in a population of laying hens. Birds could be tested in contrafreeloading trials and observed for cannibalistic tendencies by testing for their propensity to break and consume eggs, or peck at a chicken model to consume blood (e.g. Cloutier et al. 2002).

Further investigation would be needed to assess whether a propensity to perform contrafreeloading behavior is causally linked to a tendency to perform cannibalistic acts. If a causal link is established, this would provide a basis for providing enrichment that fulfills the seeking motivation as a means to prevent severe feather pecking or cannibalistic behavior in laying hens. On the other hand, we would need to ensure that providing behavioral opportunities did not stimulate cannibalism.

Contrafreeloading: information gain or a compulsion?

I have already discussed several possibilities for assessing information gain from bouts of contrafreeloading for bears (similar methods could be used for a variety of species) but it is also important to pursue alternative explanations for this seemingly sub-optimal behavior. For example, Amato and colleagues (2006, 2007) consider that contrafreeloading is compulsive-like behavior. They report that repeated application of a dopamine D2/D3 receptor agonist elevates lever pressing by rats for access to water in the presence of a water bottle providing “free” water. This behavior persists over time, whereas the information primacy hypothesis would predict contrafreeloading to decline to low levels after learning of a task that always produces the same outcome (i.e. low levels of uncertainty).

Contrafreeloading may represent a compulsive behavior that results when captive animals are not provided with behavioral opportunities to satisfy their seeking motivation. More likely, however, is that repeated administration of a dopamine receptor agonist may override the negative feedback mechanism that would normally stop contrafreeloading when there is no more information to be gained by performing the behavior. To test this hypothesis animals could be

tested for contrafreeloading tendencies after the administration of dopamine agonists is stopped. This would allow for assessment as to whether treated animals have become generally compulsive, or whether they compulsively perform contrafreeloading behavior only under the influence of the exogenous dopamine agonist. A further investigation into the relationship between contrafreeloading tendencies and compulsivity could involve assessing whether “high” contrafreeloaders show greater perseveration in tests of behavioral flexibility compared with animals performing less contrafreeloading.

Contrafreeloading in laboratory mice

The two experiments that I conducted with laboratory mice were designed to assess the strength of motivation of mice to contrafreeload. I successfully employed a new apparatus for using a consumer demand approach for assessing motivation in mice. I believe that there is value in using an animal’s natural foraging behavior in designing the tasks required for resource access, as these behaviors may encompass appetitive components that the animals are motivated to perform. In the studies described in chapter 4, tube climbing proved to be a successful method for imposing costs on mice. Utilizing a natural behavior reduced the time required for training animals to complete the demand task and, therefore, was an efficient means for assessing motivation (Cooper & Mason 2001; Olsson et al. 2002; Cooper 2004).

Mice were willing to climb tubes to access all of the foraging options provided during my two experiments. This behavior raises several questions; namely, are mice highly motivated to access these resources or was our range of costs insufficient to assess motivational strength? And, what do mice gain from continuous exploration of all resources?

My apparatus: some limitations

Imposing a wide range of costs

One limitation to imposing cost by allowing animals to climb through tubes of varying inclines was that it was that the maximum cost that could be imposed was a vertical climb. This limited our ability to assess motivational strength. In the future, cost could be further increased by extending the length of the tubes so that a mouse would be required to endure longer vertical climbs in order to access resources. With this method, it would be possible to impose a wider range of costs and therefore tease out the maximum price animals are willing to pay to reach resources.

Quantifying time budgets

A second limitation is assessing motivation during short tests as opposed to part of a complete behavioral time budget. It may be useful to test animals in closed economies (e.g. Mason et al. 2001) where they live in the test apparatus and do not have access to the motivational resources being tested except by working for them. If I had housed mice in the test apparatus for an extended period of time, I may have seen an entirely different interaction with the resources than I observed with my short test approach. Future work using a closed economy approach may paint a better picture of how contrafreeloading fits into the everyday lives of animals. Alternatively, providing continual access to contrafreeloading opportunities may facilitate rapid information gain. It may, therefore, be necessary to provide novel contrafreeloading opportunities on a regular basis to assess motivational strength for the behavior.

What do mice gain from exploring food and non-food resources?

The studies conducted by Bean and colleagues (1999) and Lindqvist and colleagues (2002) tested animals for their knowledge of the location and associated quantity of food at variable patches. It would be interesting to test for other types of knowledge gain resulting from contrafreeloading bouts as a means to quantify the breadth of this behavior as a tool for acquiring information. For example, one could test for the acquisition of specific foraging skills (as proposed above for bears) and knowledge of about food quality (in relation to food spoilage), and assess contrafreeloading as a possible mechanism for animals to learn to identify new food items (distinguish food from non-food).

For wild animals facing fluctuations in food abundance in an unstable environment, intrinsic exploration may create situations in which there is an opportunity to acquire biologically useful information (Berylne 1960; Day et al. 1998; Inglis 2000). Intrinsic exploration may facilitate the identification of new food items (Day et al. 1998) by fulfilling a motivation for animals to seek information about originally novel stimuli. Observations of intrinsic exploration often describe subjects placing novel stimuli in their mouth (Wright 1991; Renner & Seltzer 1994; Day et al. 1998), a behavior that may help in identifying novel items as food or non-food. If contrafreeloading is associated with novel food items, it may not only provide a means for animals to gather information about alternative food sources (Inglis & Ferguson 1986; Forkman 1993; Inglis et al. 1997), but may serve also as a behavioral mechanism for learning to distinguish food items from non-food items.

In the second experiment described in chapter 4, mice that had the opportunity to work for access to whole sunflower seeds or empty hulls that had been removed from sunflower seeds spent more time manipulating empty hulls. It is notable that these mice also passed up the opportunity to manipulate freely available seeds by choosing to climb tubes to access empty hulls. This might be a case of contrafreeloading where information is acquired to help mice in distinguishing ‘edible’ objects from ‘inedible’ objects. This hypothesis could be examined by designing a contrafreeloading scenario where novel free food (e.g. very small round seeds) and food (the same seeds) mixed with novel non-food items (e.g. very small round non-toxic beads that resemble the seeds) are provided and animals are later tested for their ability to distinguish the food from non-food items.

If contrafreeloading serves as a tool for animals to learn about new food items, it may have implications for introducing new food to animals in captivity. It has been observed that when a new diet formulation, or a new batch of the same diet formulation, is presented to poultry, there is a transitory suppression of feeding. It appears that the birds do not recognize the food as being edible, or classify it as being ‘unknown’ (Haskell et al. 2001). The birds may see the new forage as “not food” based on their perception of the properties “food” should have. Providing the new food in a contrafreeloading paradigm where direct comparisons could be made between new and old food items and choices are available that provide an element of control to the animal, may help to introduce new food items into an animals diet.

What the future might hold

In developing a future research program, I plan to continue to investigate environmental enrichment as a means to improve the welfare of captive animals, with a particular focus on animal motivation and seeking behavior. Little is known about motivation in relation to a wide variety of behaviors performed by animals in captivity. An increased understanding of the underlying origins of specific behaviors can yield insight into important elements to consider in housing captive animals in a manner that promotes psychological well-being.

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