

RESEARCH ARTICLE

Contrafreeloading in Grizzly Bears: Implications for Captive Foraging Enrichment

Ragen T. S. McGowan,^{1*} Charles T. Robbins,² J. Richard Alldredge,³ and Ruth C. Newberry¹

¹*Center for the Study of Animal Well-being, Department of Animal Sciences and Department of Veterinary and Comparative Anatomy, Pharmacology and Physiology, Washington State University, Pullman, Washington*

²*Department of Natural Resource Sciences and Department of Zoology, Washington State University, Pullman, Washington*

³*Department of Statistics, Washington State University, Pullman, Washington*

Although traditional feeding regimens for captive animals were focused on meeting physiological needs to assure good health, more recently emphasis has also been placed on non-nutritive aspects of feeding. The provision of foraging materials to diversify feeding behavior is a common practice in zoos but selective consumption of foraging enrichment items over more balanced “chow” diets could lead to nutrient imbalance. One alternative is to provide balanced diets in a contrafreeloading paradigm. Contrafreeloading occurs when animals choose resources that require effort to exploit when identical resources are freely available. To investigate contrafreeloading and its potential as a theoretical foundation for foraging enrichment, we conducted two experiments with captive grizzly bears (*Ursus arctos horribilis*). In Experiment 1, bears were presented with five foraging choices simultaneously: apples, apples in ice, salmon, salmon in ice, and plain ice under two levels of food restriction. 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, but all bears spent more time manipulating ice containing salmon or apples than plain ice regardless of level of food restriction. In Experiment 2, food-restricted bears were presented with three foraging choices simultaneously: apples, apples inside a box, and an empty box.

*Correspondence to: Ragen T. S. McGowan, Nestlé Purina PetCare, Product Technology Center, 3916 Pettis Road, St. Joseph, MO 64503. E-mail: Ragen.Trudelle-SchwarzMcGowan@rdmo.nestle.com

Received 27 January 2009; Accepted 16 June 2009

DOI 10.1002/zoo.20282

Published online 8 October 2009 in Wiley Online Library (wileyonlinelibrary.com).

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. Our findings support the provision of contrafreeloading opportunities as a foraging enrichment strategy for captive wildlife. *Zoo Biol* 29:484–502, 2010. © 2009 Wiley-Liss, Inc.

Keywords: animal welfare; exploration; foraging behavior

INTRODUCTION

A primary challenge in housing captive wildlife is the development of feeding protocols that meet both the physiological and psychological needs of the animals. The difficulty comes in providing nutritionally balanced diets that stimulate and challenge captive inhabitants in a manner akin to their wild counterparts [Morgan and Tromborg, 2007]. Experimental evidence suggests that a motivation to perform appetitive behavior persists among mammals and birds living in captive environments [Hughes and Duncan, 1988; Friend, 1989; Jensen and Toates, 1993; Haskell et al., 1996; Mench, 1998; Sherwin et al., 2004; de Jonge et al., 2008], with neurobiological underpinnings in the seeking circuitry of the brain that gives rise to exploration [Panksepp, 1998]. Though appetitive behavior is routinely performed to attain goals (e.g. food, shelter, mates), achievement of consummative goals is not required for the continued performance of appetitive behavior [Tarou and Bashaw, 2007] and frustration of seeking motivation may lead to its expression in undesirable forms such as stereotyped pacing [Clubb and Mason, 2003].

Animals are generally recognized as maximizers, making choices that increase the ratio of energy gain to expenditure during foraging endeavors [MacArthur and Pianka, 1966; Stephens and Krebs, 1986; Alm et al., 2002; Klaassen et al., 2006], so any departure from an optimal foraging strategy deserves investigation. Contrafreeloading, the choice to work for resources when identical resources are simultaneously available in free form, is one such departure. Though the phenomenon of contrafreeloading has been documented in several mammalian and avian species in captivity [Osborne, 1977; Inglis et al., 1997], 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 artifact of captivity. Alternatively, it may represent an adaptive form of exploration whereby animals seek information about alternative resources through sampling.

A theoretical scaffold for the phenomenon of contrafreeloading, information primacy [Woodworth, 1958; Inglis, 1983, 2000] explains animal foraging decisions based on the interplay between reducing environmental uncertainty and satiating immediate needs. Inglis et al. [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 in predicting contrafreeloading events. The limited data supporting the information primacy hypothesis for contrafreeloading have come from domestic rodents and captive and domestic birds [Inglis and Ferguson, 1986; Forkman, 1991, 1993, 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), studies of contrafreeloading in captive mammalian wildlife other than primates are absent from the literature.

Foraging materials and devices that require an animal to work to obtain food are offered to wild mammals in captivity as a means to diversify foraging behavior (Table 1), an approach that often involves the introduction of treat items [Honest and Marin, 2006]. However, selective consumption of foods provided for foraging enrichment over more balanced “chow” diets can lead to nutrient imbalance [NRC, 1996; Wolfensohn and Honest, 2005]. Providing captive animals with opportunities to contrafreeload could satisfy seeking motivations associated with food acquisition while maintaining the nutrient composition of balanced diets. Furthermore, whereas 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; Van de Weerd et al., 2006], thus constituting 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 and Mason, 2007], general exploration or cognitive challenge [Meehan and Mench, 2007] than on appetitive components of foraging behavior, specifically. A more complete understanding of the characteristics of beneficial foraging opportunities and the principles underlying their effectiveness is called for.

In this article, we explore contrafreeloading behavior 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 behavior in response to concealed food, utilizing a species and mode of earning food not previously investigated in contrafreeloading studies. If contrafreeloading enables animals to gather information about food resources that could be exploited to a greater extent at times when more readily accessible food is unavailable, it is reasonable to hypothesize that grizzly bears would demonstrate this behavior. 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. To test these predictions, we conducted two experiments, one involving working for food frozen within ice blocks and one involving working for food concealed in cardboard boxes.

It is becoming 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 et al., 1998, p 1]. An internet search for zoological parks and sanctuaries worldwide that house bears revealed 65 facilities with English web sites that reported using ice blocks containing food as enrichment

TABLE 1. Survey of effects of foraging enrichment techniques incorporating “working” for food on commonly reported dependent variables, across a range of wild mammals held in captivity^a

Method	Species	Common name	Outcome					References
			Foraging behavior	Abnormal behavior	Agonistic behavior	Time spent active		
Sound activated “Fish Catapult”	<i>Ursus maritimus</i>	Polar Bear	+	–	–	+	Markowitz [1982]	
Food inside ice blocks	<i>Ursus arctos</i>	Kodiak Bear	NR	–	NM	+	Forthman et al. [1992]	
	<i>Ursus middendorffii</i>	Polar Bear	NR	V	NM	+	Forthman et al. [1992]	
Fresh browse	<i>Ailuropoda melanoleuca</i>	Giant Panda	+	V	NM	+	Swaisgood et al. [2001, 2005]	
	<i>Selenarctos tibetanus</i>	Asiatic Black Bear	NR	V	NM	+	Forthman et al. [1992]	
	<i>Gorilla gorilla gorilla</i>	Western Lowland gorilla	+	NS	–	+	Rooney and Sleeman [1998]	
	<i>Ailuropoda melanoleuca</i>	Giant Panda	+	V	NM	+	Swaisgood et al. [2001, 2005]	
Food in cardboard box	<i>Gorilla gorilla gorilla</i>	Western Lowland Gorilla	+	NS	–	+	Rooney and Sleeman [1998]	
	<i>Melursus urinus</i>	Sloth	–	–	NM	NS	Carlstead et al. [1991]	
Filled logs	<i>Ursus americanus</i>	Black Bear	NS	NS	NM	NS	Carlstead et al. [1991]	
	Various species	Primates	+	V	V	+	Fekete et al. [2000]; Honess and Marin [2006] ^b	
Foraging boards—Astroturf, fleece, etc.	<i>Ailuropoda melanoleuca</i>	Giant Panda	+	V	NM	+	Swaisgood et al. [2001, 2005]	
			+	NM	V	+		
Puzzle feeder								

TABLE 1. Continued

Method	Species	Common name	Outcome				References
			Foraging behavior	Abnormal behavior	Agonistic behavior	Time spent active	
Dispersing food throughout enclosure	<i>Papio hamadryas hamadryas</i>	Hamadryas Baboon					Jones and Pillay [2004]
	<i>Ursus americanus</i>	Black Bear	+	-	NM	NS	Carlstead et al. [1991]
Mechanical feeding tree	<i>Felis bengalensis</i>	Leopard Cat	+	-	NM	+	Shepherdson et al. [1993]
	<i>Elephas maximus</i>	Asian Elephant	NS	NM	NM	NS	Weidemayer [1998]
	<i>Tremarctos ornatus</i>	Spectacled Bear	+	NS	NM	+	Fischbacher and Schmid [1999]
	<i>Ursus arctos</i>	Brown Bear	+	-	NM	+	Morimura and Ueno [1999]
Electronic feeding box	<i>Vicugna vicugna</i>	Vicugna	+	+	NM	+	Parker et al. [2006]
	<i>Ursus americanus</i>	Black Bear	+	NS	NM	NS	Carlstead et al. [1991]
Food in basket, cage, or net	<i>Panthera tigris altaica</i>	Amur Tiger	+	V	NM	V	Jenny and Schmid [2002]
	<i>Eulemur macaco macaco</i> ; <i>Lemur catta</i>	Black Lemur; Ringtail Lemur	NS	-	NM	+	Maloney et al. [2006]
Food inside bag —paper or cloth	<i>Gorilla gorilla gorilla</i>	Western Lowland Gorilla	+	NS	-	+	Rooney and Sleeman [1998]
	<i>Ailuropoda melanoleuca</i>	Giant Panda	+	V	NM	+	Swaisgood et al. [2001, 2005]
Mixing food in substrate (e.g. woodchips, gravel, or sand)	<i>Macaca arctoides</i>	Stump-tailed Macaque	+	-	-	+	Chamove et al. [1982]; Wolfensohn and Honess [2005]

<i>Odobenus rosmarus divergens</i>	Pacific Walrus	+	-	NM	+	Kastelein and Wiepkema [1989]
<i>Pan troglodytes</i>	Chimpanzee	+	-	-	+	Baker [1997]
<i>Cercocebus torquatus torquatus</i>	Red-capped Mangabey	+	-	V	+	Blois-Heulin and Jubin [2004]
<i>Papio hamadryas hamadryas</i>	Hamadryas Baboon	+	NM	-	+	Jones and Pillay [2004]
<i>Eulemur macaco macaco; Lemur catta</i>	Black Lemur; Ringtail Lemur	NS	-	NM	+	Maloney et al. [2006]
Termite mound	Chimpanzee	+	-	NM	+	Maki et al. [1989]; Howell and Fritz [1990] ^b
Carcass feeding	Various	V	-	V	V	Young [1997] ^b ; Houts [1999] ^b ; McPhee [2002]
	<i>Acinonyx jubatus</i>	+	NM	NM	+	Bond and Lindburg [1990]
Live prey	<i>Suricata suricata</i>	+	NS	NM	+	Shepherson et al. [1989]
	<i>Felis viverrina</i>	+	NS	NM	+	Shepherdson et al. [1993]
	<i>Panthera tigris sumatrae</i>	+	NS	NM	NS	Bashaw et al. [2003]
	<i>Eulemur macaco macaco; Lemur catta</i>	NS	-	NM	+	Maloney et al. [2006]

^aDatabases searched: Science Direct, Biosis, Web of Science, Scirus, AGRICOLA. Keywords: contrafreeloading; foraging enrichment; environmental enrichment; Behavioral enrichment; working for food; feeding; foraging behavior; captive animals. Outcomes: +, increase; -, decrease; V, variable; NS, not significant; NR, not reported; NM, not measured.

^bPapers reviewing effects without presenting statistics.

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.

Ice blocks have been reported to add diversity to foraging opportunities [Forthman et al., 1992; Grindrod and Cleaver, 2001; Swaisgood et al., 2001; Renner and Lussier, 2002]. However, ours is the first controlled study, to our knowledge, to provide a simultaneous choice between plain ice, free food, and food of the same type concealed in ice, enabling us to tease out the relative attractiveness of these elements. Our aim in Experiment 1 was to examine contrafreeloading behavior in grizzly bears by providing them the opportunity to work for food through extracting concealed items from inside ice blocks. We examined the hunger component of the model proposed by Inglis et al. [1997, 2001] by manipulating food restriction levels before 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.

To obtain further information about the propensity of bears to contrafreeload, we reduced the level of effort required to extract concealed food by replacing ice blocks with cardboard boxes in Experiment 2. Cardboard boxes are often employed as enrichment devices for captive wild and domestic animals due to their malleable, destructible and nontoxic 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.

MATERIALS AND 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 × 3.3 m²) 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 07.00 and 15.00 hr 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 07.00 hr and given a small food reward at 15.00 hr 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.

Experiment 1: Smash and Grab—the Ice Block Challenge

Experiment 1 was conducted between late August and early October with four wild born adult grizzly bears, Bo and Irving (17-year-old brothers, weighing approximately 305 kg) and June and Patches (unrelated 16-year-old females, weighing approximately 185 kg). Starting three days before the commencement of behavioral trials, each bear was housed temporarily in an indoor–outdoor pen and given a diet consisting of salmon and apples fed at 30% of ad libitum intake, a level typical for nonlactating adult bears in this facility. They were temporarily denied access to the semi-natural enclosure to prevent additional food intake through foraging on clover and grasses. Bears experience brief periods of individual housing on occasion for other studies at this facility and habituated quickly to this condition. Behavioral trials were conducted in the indoor portion of the pen, where visual isolation from other bears prevented social learning of foraging preferences and tactics. It also provided uniformity in temperature and light intensity during testing of different individuals.

Each bear was subjected to two experimental treatments: (1) food restriction (30% of ad libitum) and (2) ad libitum food and was in the study for 14 days. Following three days of habituation, three 1 hr foraging choice trials under the food restriction condition were conducted over the next three days (one trial per day). 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, for a total of six 1 hr trials. The duration of the experiment was limited to avoid adverse consequences from confinement and social restriction.

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, *Malus pumila*), (2) free salmon (a pile of frozen Chinook salmon, *Oncorhynchus tshawytscha*), (3) a plain ice block, (4) earned apples (a mixture of Fuji and Macintosh apples frozen inside an ice block) and (5) earned salmon (Chinook 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.

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

Trials were conducted at 07.00 hr 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 hr to minimize the

amount of ice that melted, as 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 [Robbins et al., 2007]. 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.

Experiment 2: Rip and Shred—Does Less Effort Propel the Choice to Work?

Experiment 2 was conducted from late April through May. Subjects 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. The bears 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 07.00 hr. They were accustomed to eating apples before the experiment.

Each bear participated in three 1 hr trials (one trial per day), with two bears being tested consecutively each morning. 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 apples (approximately 0.04 kg/kg body weight) were enclosed in a brown cardboard box (45.7 cm long × 45.7 cm wide × 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

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 in Experiment 1, the pieces were collected for weigh back. During each trial, a Psion Workabout[®] handheld computer (Psion PLC, London, United Kingdom) equipped with The Observer[®] Version 4.0 (Noldus Information Technology, Wageningen, The Netherlands) was used to record each focal animal's behavior continuously for 1 hr by direct observation through an observation window. All transitions between noncontact investigation, manipulation of each foraging choice and other behavior (Table 2) were recorded, from which the total time spent in each behavior category per hour was calculated. All data were collected by the same observer.

Statistical Analysis

Data for noncontact investigation, manipulation, and consumption were analyzed separately for each experiment. We used a mixed linear model (Proc Mixed) of the SAS Institute [1999], with foraging choice as a repeated measure, to assess the

TABLE 2. Ethogram

Behavior category	Description	Definitions of behavioral elements occurring within each category
Noncontact 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 it toward pen wall or floor Chew: bear's jaw moves vertically crushing substance
Null	Behavior 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

effects of sex, trial (1–6 in Experiment 1; 1–3 in Experiment 2) and their interactions on the bears' behavior toward the foraging options. Bear within sex, and bear by trial within sex, were random terms in the model, and the subject effect was bear by trial. A contrast statement was used to assess effects of food restriction across trials in Experiment 1. 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.

RESULTS

Experiment 1

Investigation and manipulation

Bears approached and began to explore the foraging choices immediately upon admittance to the test arena. During initial noncontact investigation, bears typically spent 2–3 sec 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 noncontact 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: $t_{68} \geq 2.04$, $P < 0.05$; Fig. 1). There were no differences in noncontact 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: $F_{4,68} = 36.09$, $P < 0.0001$; Fig. 2). Bears spent significantly more time manipulating free apples and salmon than ice blocks containing these foods (Tukey adjusted t test: $t_{68} \geq 3.4$, $P \leq 0.010$; Fig. 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: $t_{68} \geq 3.4$, $P \leq 0.010$; Fig. 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: $F_{1,15} = 0.91$, $P = 0.36$), 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.

Consumption

Two bears (Bo and June) were successful in accessing food extracted from ice blocks, all of which were consumed. Bo broke ice blocks open by picking them up and tossing them against the wall of the test arena while June pawed at and chewed ice blocks until the food within was exposed. We found no effects of sex

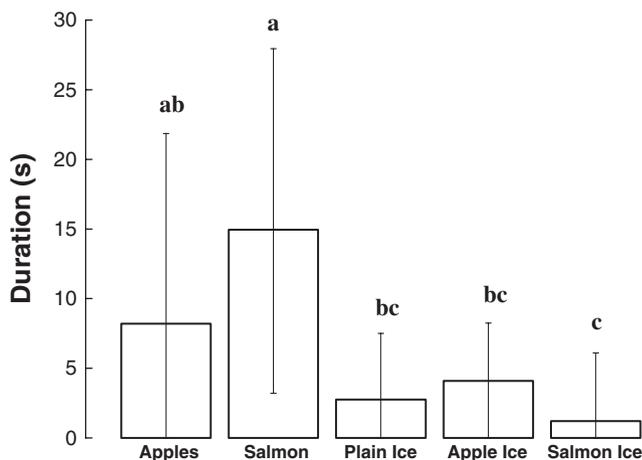


Fig. 1. Median (\pm inter-quartile range) time bears ($n = 4$) spent in noncontact investigation of five foraging options. Letters indicate differences ($P < 0.05$).

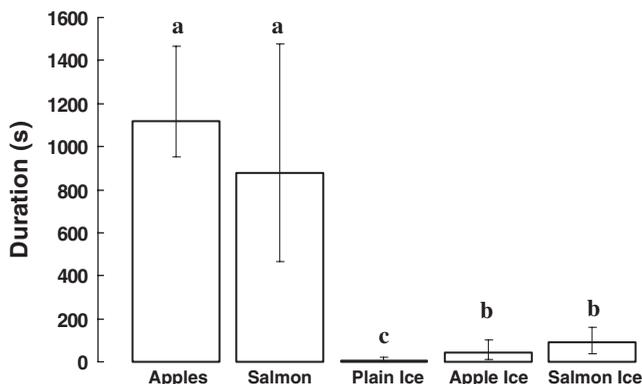


Fig. 2. Median (\pm inter-quartile range) time bears ($n = 4$) spent manipulating five foraging options. Letters indicate differences ($P < 0.05$).

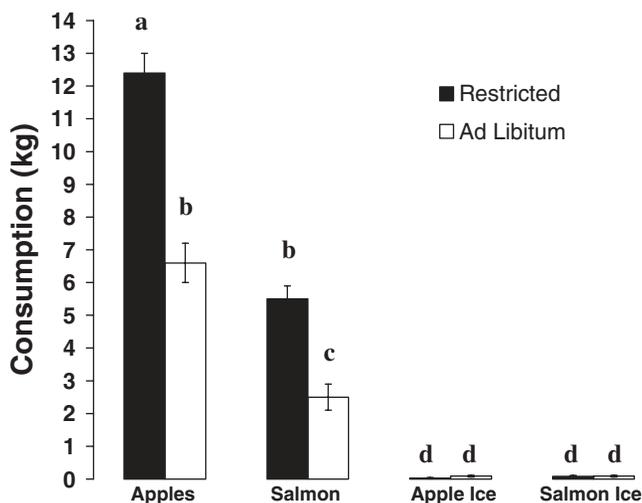


Fig. 3. Mean (\pm SE) consumption of four food options (Apples, Salmon, Apples from ice, Salmon from ice) by bears ($n = 4$) during application of two food treatments. Letters indicate differences ($P < 0.05$) across food treatments and options.

(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 hr test sessions (Fig. 3). 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 hr trials when fed ad libitum than when food was restricted (Fig. 3).

Experiment 2

Investigation and manipulation

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 noncontact investigation did not differ between the free apples (mean \pm SE, 12.9 ± 2.3 sec), the earned apples (13.7 ± 2.3 sec), and the empty box (14.0 ± 3.3 sec) (Mixed linear model: $F_{2,28} = 0.60$, $P = 0.56$). We found no significant effect of sex (Mixed linear model: $F_{1,4} = 5.12$, $P = 0.086$) or trial ($F_{2,10} = 1.24$, $P = 0.33$) on noncontact investigation.

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: $F_{2,28} = 14.24$, $P < 0.0001$; Fig. 4). 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 ($t_{28} = 3.86$, $P = 0.0017$; Fig. 4). 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 showing no significant difference in time spent manipulating boxes with apples (mean \pm SE, 729.5 ± 92.4 sec) and free apples (321.7 ± 64.4 sec; Tukey adjusted t test: $t_{28} = -1.35$, $P = 0.19$) and the four adult females spending more time manipulating free apples (1271.4 ± 47.7 sec) than boxes with apples (331.6 ± 55.4 sec; Tukey adjusted t test: $t_{28} = 4.63$, $P = 0.001$).

Consumption

Five bears were successful in extracting and consuming food concealed inside boxes (two males and three 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

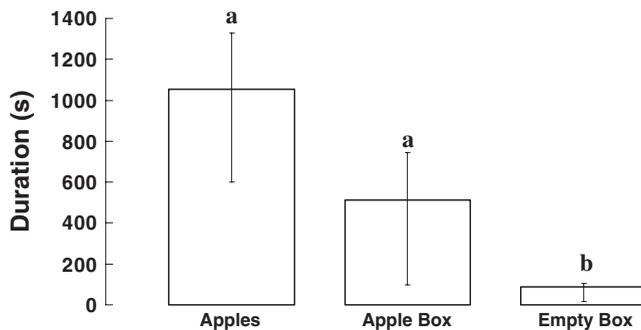


Fig. 4. Median (\pm inter-quartile range) time bears ($n = 6$) spent manipulating three foraging options. Letters indicate differences ($P < 0.05$).

on one occasion when 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 onto 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.

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 hr 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

As predicted, captive grizzly bears spent time manipulating concealed foods in the presence of unconcealed (“free”) foods of the same type when presented with a contrafreeloading paradigm. 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 manipulating concealed food resources.

The majority of published contrafreeloading studies involve a scenario where animals are provided with the opportunity to work for food while the same food is simultaneously available in free form. 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 [$> 50\%$, e.g. Lindqvist and Jensen, 2008] of total food consumed. Defining contrafreeloading based on some proportion of earned food consumed excludes studies which explore the phenomenon using non-nutritive resources [e.g. Singh, 1970; Baenninger and Mattleman, 1973; 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, indicating that effort in resource acquisition does not directly parallel resource consumption [e.g. Neuringer, 1969; Inglis and Shepherd, 1994; Amato et al., 2006]. Given that optimal foraging models predict an absolute preference for consuming easily obtained food over food requiring effort to exploit, any deviation from this prediction requires an alternate explanation [Stephens and

Krebs, 1986; Inglis et al., 1997]. 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. By this measure, all of the grizzly bears engaged in contrafreeloading in our experiments.

The “fuzzy model” [Inglis et al., 1997, 2001] predicts that contrafreeloading should arise as physiological needs decrease. We investigated the effects of “physiological need” on contrafreeloading by testing bears under two levels of food restriction. Contrary to our prediction, 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 leading up to 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 been associated with greater hunger than the ad libitum condition. It is unlikely that our attempt to satiate the ad libitum-fed bears failed given that the bears were allowed to feed freely for five days before testing under this condition. During this time, the amount of food consumed each day decreased and latency to approach free food increased, a pattern consistent with a decreasing hunger level [Lawrence et al., 1988; Vickery and Mason, 2005]. It is possible that our low sample size may not have allowed for a detection of food restriction effects on contrafreeloading although we did detect increased consumption of free apples and salmon by the food-restricted vs. ad libitum-fed bears. Alternatively, the motivation of grizzly bears to engage in contrafreeloading may be less affected by physiological need than predicted, a finding that would correspond with studies of carnivores suggesting that the decision whether or not to hunt is independent of hunger level [e.g. cheetahs, Cooper et al., 2007]. The lack of difference in contrafreeloading levels between food-restricted and ad libitum-fed bears may also reflect changes in motivation before hibernation. If the main function of contrafreeloading is to collect information about the environment that can be used during future foraging endeavors [Inglis et al., 1997, 2001], we might expect an individual close to hibernation to partake less in this behavior as information gathered would be of little use in the near future.

The “fuzzy model” of contrafreeloading [Inglis et al., 1997, 2001] predicts that an increase in the effort required to exploit earned food items will lead to a reduction in contrafreeloading. In Experiment 1, 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 hr per day on 6 days) resulting in limited success by bears in their attempts to extract earned food items. Although longer observation periods would have enabled extraction of additional food from ice blocks [Renner and Lussier, 2002], we limited the duration of observations to control for melting of ice in hot weather. In Experiment 2, we concealed food inside cardboard boxes to provide bears with a task that required less effort than breaking ice blocks. 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].

Seasonal differences in motivation to explore, individual animal differences, and differences in number of foraging choices presented in the two experiments may have also contributed to increased manipulation times of cardboard boxes in Experiment 2 compared with ice blocks in Experiment 1.

Several authors have examined the effects of age on exploration and interaction with enrichment items and the results are wide ranging [e.g. Swaisgood et al., 2001; Kuba et al., 2006]. In our study, male sub-adult bears manipulated and tended to consume more earned than free food items in contrast to adult bears who manipulated and consumed more free than earned food items. Similarly, Lindqvist and Jensen [2008] observed more contrafreeloading in young than sexually mature domestic and jungle fowl. In terms of information gain, these findings are logical as younger animals have more to learn about their environment than older animals. For sub-adult animals 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 [Crocket, 1987]. Contrafreeloading may also reflect an attraction toward risk [Spear, 2000], or “temptation to gamble” [Adriani and Laviola, 2006] given that it involves choosing resources that are uncertain when more reliable resources are available. In our study, greater contrafreeloading by the sub-adult males than the adult bears may reflect increased willingness to take risks, and having more to learn from such risks. Nevertheless, these interpretations remain speculative given that age, sex, and relatedness were confounded in our limited bear population.

Although contrafreeloading behavior would have adaptive benefits in the wild, it could seem “unnecessary” in captive animals reliably provided with food. Yet captive and domesticated animals retain a strong internally driven motivation to explore and learn about environmental contingencies [Panksepp, 1998; Inglis, 2000; Everitt et al., 2001; Spruijt et al., 2001]. A lack of opportunity to express this behavior in a constructive manner may lead to negative emotional consequences and abnormal behavior [Clubb and Mason, 2003]. Theory and empirical evidence suggest that animal well-being is enhanced by providing animals with appropriate challenges [Meehan and Mench, 2007; Morgan and Tromborg, 2007] and choices in their environment [Carlstead, 1996; Markowitz and Aday, 1998; Owen et al., 2005; Ross, 2006; Van de Weerd et al., 2006], all of which can be achieved through the provision of contrafreeloading opportunities.

CONCLUSIONS

1. Grizzly bears in our study demonstrated a greater attraction towards concealed food items that could be extracted from destructible objects over 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].
2. Grizzly bears contrafreeloaded both when fed ad libitum and when feed restricted.
3. Contrafreeloading by grizzly bears was observed in both sexes over a wide age range.

4. In cases where there are concerns about nutritional imbalance resulting from foraging enrichment for captive wildlife, our results suggest that provision of contrafreeloading opportunities may be useful for enabling satisfaction of seeking motivation, providing animals with an element of control over their environment, and offering cognitive challenge.

ACKNOWLEDGMENTS

The authors thank the staff of the Washington State University Bear Research, Education, and Conservation Facility for their dedicated care of the grizzly bears and the R. B. Tukey Horticulture Orchard for donation of apples.

REFERENCES

- Adriani W, Laviola G. 2006. Delay aversion but preference for large and rare rewards in two choice tasks: implications for the measurement of self-control parameters. *BMC Neurosci* 7:52.
- Alm U, Birgersson B, Leimar O. 2002. The effect of food quality and relative abundance on food choice in fallow deer. *Anim Behav* 64:439–445.
- Amato D, Milella MS, Badiani A, Nencini P. 2006. Compulsive-like effects of repeated administration of quinpirole on drinking behavior in rats. *Behav Brain Res* 172:1–13.
- Baenninger R, Mattleman RA. 1973. Visual reinforcement: operant acquisition in the presence of a free mirror. *Anim Learn Behav* 1: 302–306.
- Baker KC. 1997. Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. *Zoo Biol* 16:225–236.
- Bashaw MJ, Bloomsmith MA, Marr MJ, Maple TL. 2003. To hunt or not to hunt? A feeding enrichment experiment with captive large felids. *Zoo Biol* 22: 189–198.
- Bean D, Mason GJ, Bateson M. 1999. Contrafreeloading in starlings: testing the information hypothesis. *Behaviour* 136:1267–1282.
- Blois-Heulin C, Jubin R. 2004. Influence of the presence of seeds and litter on the behaviour of captive red-capped mangabeys *Cercocebus torquatus torquatus*. *Appl Anim Behav Sci* 85:349–362.
- Bond JC, Lindburg DG. 1990. Carcass feeding of captive cheetahs (*Acinonyx jubatus*): the effects of a naturalistic feeding program on oral health and psychological well-being. *Appl Anim Behav Sci* 26:373–382.
- Carlstead K. 1996. Effects of captivity on the behavior of wild mammals. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. *Wild Mammals in captivity*. Chicago, IL: University of Chicago Press. p 317–333.
- Carlstead K, Seidensticker J, Baldwin R. 1991. Environmental enrichment for zoo bears. *Zoo Biol* 10:3–16.
- Chamove AS, Anderson JR, Morgan-Jones SC, Jones SP. 1982. Deep woodchip litter: hygiene, feeding, and behavioural enhancements in eight primate species. *Int J Study Anim Probl* 3:308–318.
- Clubb R, Mason G. 2003. Captivity effects on wide-ranging carnivores. *Nature* 425:473–474.
- Clubb R, Mason G. 2007. Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. *Appl Anim Behav Sci* 102:303–328.
- Cooper AB, Pettorelli N, Durant SM. 2007. Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. *Anim Behav* 73:651–659.
- Crockett CM. 1987. Diet, dimorphism and demography: perspectives from howlers to hominids. In: Kinzey WG, editor. *The evolution of human behavior: primate models*. Albany, NY: State University of New York Press.
- de Jonge FH, Tilly S-L, Baars AM, Spruijt BM. 2008. On the rewarding nature of appetitive feeding behaviour in pigs (*Sus scrofa*): do domesticated pigs contrafreeload? *Appl Anim Behav Sci* 114:359–372.
- Everitt BJ, Dickinson A, Robbins TW. 2001. The neuropsychological basis of addictive behaviour. *Brain Res Rev* 36:129–138.
- Fekete JM, Norcross JL, Newman JD. 2000. Artificial turf foraging boards as environmental enrichment for pair-housed female squirrel monkeys. *Contemp Top Lab Anim* 39:22–26.
- Fischbacher M, Schmid H. 1999. Feeding enrichment and stereotypic behavior in spectacled bears. *Zoo Biol* 18:363–371.
- Forkman B. 1991. Some problems with current patch-choice theory: a study on the Mongolian gerbil. *Behaviour* 117:243–254.
- Forkman B. 1993. The effect of uncertainty on the food intake of the Mongolian gerbil. *Behaviour* 124:197–206.
- Forkman B. 1996. The foraging behaviour of Mongolian gerbils: a behavioural need or a need to know? *Behaviour* 133:129–143.
- Forthman DL, Elder SD, Bakeman R. 1992. Effects of feeding enrichment on behavior of three species of captive bears. *Zoo Biol* 11:187–195.

- Friend T. 1989. Recognizing behavioral needs. *Appl Anim Behav Sci* 22:151–158.
- Grindrod JAE, Cleaver JA. 2001. Environmental enrichment reduces the performance of stereotypic circling behaviour in captive common seals (*Phoca vitulina*). *Anim Welfare* 10:53–63.
- Haskell MJ, Terlouw EMC, Lawrence AB, Erhard HW. 1996. The relationship between food consumption and persistence of post-feeding foraging behaviour in sows. *Appl Anim Behav Sci* 48:249–262.
- Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT. 1999. Effect of seasonal difference in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Can J Zool* 77:1623–1630.
- Honess PE, Marin CM. 2006. Enrichment and aggression in primates. *Neurosci Biobehav Rev* 30:413–436.
- Houts L. 1999. Supplemental carcass feeding for zoo carnivores. *Shape Enrich* 8.
- Howell S, Fritz J. 1999. The nuts and bolts of captive chimpanzee diets and food as enrichment: a survey. *J Appl Anim Welf Sci* 2:205–215.
- Hughes BO, Duncan IJH. 1988. The notion of ethological “need”, models of motivation and animal welfare. *Anim Behav* 36:1696–1707.
- Inglis IR. 1983. Towards a cognitive theory of exploratory behaviour. In: Archer J, Burke L, editors. *Exploration in Animals and Humans*. London: Van Nostrand Reinhold. p 72–116.
- Inglis IR. 2000. The central role of uncertainty reduction in determining behaviour. *Behaviour* 137:1567–1599.
- Inglis IR, Ferguson NJK. 1986. Starlings search for food rather than eat freely-available, identical food. *Anim Behav* 34:614–617.
- Inglis IR, Shepherd DS. 1994. Rats work for food they then reject: support for the information-primacy approach to learned industriousness. *Ethology* 98:154–164.
- Inglis IR, Forkman B, Lazarus J. 1997. Free food or earned food? a review and fuzzy model of contrafreeloading. *Anim Behav* 53:1171–1191.
- Inglis IR, Langton S, Forkman B, Lazarus J. 2001. An information primacy model of exploratory and foraging behaviour. *Anim Behav* 62:543–557.
- Jenny S, Schmid H. 2002. Effect of feeding boxes on the behavior of stereotyping Amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. *Zoo Biol* 21:573–584.
- Jensen P, Toates FM. 1993. Who needs “behavioural needs”? Motivational aspects of the needs of animals. *Appl Anim Behav Sci* 37:161–181.
- Jones M, Pillay N. 2004. Foraging in captive hamadryas baboons: implications for enrichment. *Appl Anim Behav Sci* 88:101–110.
- Kastelein RA, Wiepkema PR. 1989. A digging trough as occupational therapy for Pacific walrus (*Odobenus rosmarus divergens*) in human care. *Aqua Mam* 15:9–17.
- Klaassen RHG, Nolet BA, van Gils JA, Bauer S. 2006. Optimal movement between patches under incomplete information about the spatial distribution of food items. *Theor Popul Biol* 70:452–463.
- Kopp J, Bourland G, Tarte RD, Vernon CR. 1976. Acquisition of barpressing in non-deprived rats. *Psychol Rec* 26:49–54.
- Kuba MJ, Byrne RA, Meisel DV, Mather JA. 2006. When do octopuses play? Effects of repeated testing, object type, age and food deprivation on object play in *Octopus vulgaris*. *J Comp Psychol* 120:184–190.
- Lawrence AB, Appleby MC, Illius AW. 1988. Measuring hunger in the pig using operant conditioning: the effect of food restriction. *Anim Prod* 47:131–137.
- Lindburg DG. 1998. Enrichment of captive mammals through provisioning. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. *Second nature: environmental enrichment for captive animals*. Washington, DC: Smithsonian Institution Press. p 262–276.
- Lindqvist C, Jensen P. 2008. Effects of age, sex and social isolation on contrafreeloading in red junglefowl (*Gallus gallus*) and White Leghorn fowl. *Appl Anim Behav Sci* 114:419–428.
- Lindqvist CES, Schutz KE, Jensen P. 2002. Red junglefowl have more contrafreeloading than White Leghorn layers: effect of food deprivation and consequences for information gain. *Behaviour* 139:1195–1209.
- MacArthur RH, Pianka ER. 1966. On the optimal use of a patchy environment. *Am Nat* 100:603–609.
- Maki S, Alford PL, Bloomsith MA, Franklin J. 1989. Food puzzle device simulating termite fishing for captive chimpanzees (*Pan troglodytes*). *Am J Primatol Suppl* 1:71–78.
- Maloney MA, Meiers ST, White J, Romano MA. 2006. Effects of three food enrichment items on the behavior of black lemurs (*Eulemur macaco macaco*) and ringtail lemurs (*Lemur catta*) at the Henson Robinson Zoo, Springfield, Illinois. *J Appl Anim Welf Sci* 9:111–127.
- Markowitz H. 1982. Behavioral enrichment in the zoo. New York: Van Nostrand Reinhold.
- Markowitz H, Aday C. 1998. Power for captive animals: contingencies and nature. In: Shepherdson DJ, Mellen JD, Hutchins M, editors. *Second nature: environmental enrichment for captive animals*. Washington, DC: Smithsonian Institution Press. p 47–58.
- McPhee ME. 2002. Intact carcasses as environmental enrichment for felids: effects on on- and off-exhibit behaviors. *Zoo Biol* 21:37–47.
- Meehan CL, Mench JA. 2007. The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Appl Anim Behav Sci* 102:246–261.
- Mench JA. 1998. Environmental enrichment and the importance of exploratory behavior. In: Shepherdson DJ, Mellen JD, Hutchins M,

- editors. Second nature: environmental enrichment for captive animals. Washington, DC: Smithsonian Institution Press. p 30–46.
- Morgan KN, Tromborg CT. 2007. Sources of stress in captivity. *Appl Anim Behav Sci* 102:262–302.
- Morimura N, Ueno Y. 1999. Influences on the feeding behavior of three mammals in the Maruyama Zoo: bears, elephants, and chimpanzees. *J Appl Anim Welf Sci* 2:169–186.
- Neuringer AJ. 1969. Animals respond for food in the presence of free food. *Science* 166:399–401.
- Newberry RC. 1995. Environmental enrichment: increasing the biological relevance of captive environments. *Appl Anim Behav Sci* 44:229–243.
- NRC. 1996. Guide for the care and the use of laboratory animals. National Research Council. Washington, DC: National Academy Press.
- Osborne SR. 1977. The free food (contrafreeloading) phenomenon: a review and analysis. *Anim Learn Behav* 5:221–235.
- Owen MA, Swaisgood RR, Czekala NM, Lindburg DG. 2005. Enclosure choice and well-being in giant pandas: is it all about control? *Zoo Biol* 24:475–481.
- Panksepp J. 1998. Affective neuroscience: the foundations of human and animal emotions. New York: Oxford University Press. 466p.
- Parker M, Goodwin D, Redhead E, Mitchell H. 2006. The effectiveness of environmental enrichment on reducing stereotypic behaviour in two captive vicugna (*Vicugna vicugna*). *Anim Welf* 15:59–62.
- Renner MJ, Lussier JP. 2002. Environmental enrichment for the captive spectacled bear (*Tremarctos ornatus*). *Pharmacol Biochem Behav* 73:279–283.
- Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos* 116:1675–1682.
- Rode KD, Robbins CT, Shipley LA. 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128:62–71.
- Rooney MB, Sleeman J. 1998. Effects of selected behavioral enrichment devices on behavior of Western lowland gorillas (*Gorilla gorilla gorilla*). *J Appl Anim Welf Sci* 1:339–351.
- Ross SR. 2006. Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). *Behav Processes* 73:117–120.
- SAS Institute. 1999. SAS/STAT User's Guide, Version 8. Cary, NC: SAS Institute Inc. 3884p.
- Shepherdson DJ, Brownback T, James A. 1989. A mealworm dispenser for the slender-tailed meerkat (*Suricata suricata*) at London Zoo. *Int Zoo Yearb* 28:268–271.
- Shepherdson DJ, Carlstead K, Mellen JD, Seidensticker J. 1993. The influence of food and presentation on the behavior of small cats in confined environments. *Zoo Biol* 12:203–216.
- Shepherdson DJ, Mellen JD, Hutchins M. 1998. Second nature: environmental enrichment for captive animals. Washington, DC: Smithsonian Institution Press.
- Sherwin CM, Haug E, Terkelsen N, Vadgama M. 2004. Studies on the motivation for burrowing by laboratory mice. *Appl Anim Behav Sci* 88:343–358.
- Singh D. 1970. Preference for bar pressing to obtain reward over freeloading in rats and children. *J Comp Physiol Psychol* 73:320–327.
- Spear LP. 2000. The adolescent brain and age-related behavioral manifestations. *Neurosci Biobehav Rev* 24:417–463.
- Spruijt BM, van den Bos R, Pijlman FTA. 2001. A concept of welfare based on reward evaluation mechanisms in the brain: anticipatory behaviour as an indicator of the state of reward systems. *Appl Anim Behav Sci* 72:145–171.
- Stephens DW, Krebs JR. 1986. Foraging theory. Princeton, NJ: Princeton University Press.
- Swaisgood RR, White AM, Zhou X, Zhang H, Zhang G, Wei R, Hare VJ, Tepper EM, Lindburg DG. 2001. A quantitative assessment of the efficacy of an environmental enrichment programme for giant pandas. *Anim Behav* 61:447–457.
- Swaisgood RR, White AM, Zhou X, Zhang G, Lindburg DG. 2005. How do Giant pandas (*Ailuropoda melanoleuca*) respond to varying properties of enrichments? A comparison of behavioral profiles among five enrichment items. *J Comp Psychol* 119:325–334.
- Tarou LR, Bashaw MJ. 2007. Maximizing the effectiveness of environmental enrichment: suggestions from the experimental analysis of behavior. *Appl Anim Behav Sci* 102:189–204.
- Tarte RD. 1981. Contrafreeloading in humans. *Psychol Rep* 49:859–866.
- Van de Weerd HA, Docking CM, Day JEL, Avery PJ, Edwards SA. 2003. A systematic approach towards developing environmental enrichment for pigs. *Appl Anim Behav Sci* 84:101–118.
- Van de Weerd HA, Docking CM, Day JEL, Breuer K, Edwards SA. 2006. Effects of species-relevant environmental enrichment on the behaviour and productivity of finishing pigs. *Appl Anim Behav Sci* 99:230–247.
- Vickery SS, Mason GJ. 2005. Stereotypy and perseverative responding in caged bears: further data and analyses. *Appl Anim Behav Sci* 91:247–260.
- Weidenmayer C. 1998. Food hiding and enrichment in captive Asian elephants. *Appl Anim Behav Sci* 56:77–82.
- Wolfensohn S, Honess P. 2005. Handbook of primate husbandry and welfare. Oxford: Blackwell Publishing.
- Woodworth RS. 1958. Dynamics of behavior. New York: Holt, Rinehart and Winston.
- Young RJ. 1997. The importance of food presentation for animal welfare and conservation. *Proc Nutr Soc* 56:1095–1104.