Free food or earned food? A review and fuzzy model of contrafreeloading

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Abstract. Animals will work (e.g. lever press) for 'earned' food even though identical 'free' food can easily be obtained from a nearby dish. This phenomenon, called contrafreeloading, appears to contradict a basic tenet of most learning, motivation and optimal foraging theories; namely that animals strive to maximize the ratio of reward, or benefit, to effort, or cost. This paper reviews the factors that have been found to affect the level of contrafreeloading, to try to explain the behaviour. In experiments involving intensive training, contrafreeloading may be explained on the basis of secondary reinforcement and/or differential exposure to the alternative food sources. However, contrafreeloading also occurs without prior training. Contrafreeloading declines with increasing hunger and with increases in the effort required to obtain the earned food: it also has an inverted-U relationship with the degree of stimulus change associated with the earned food. A fuzzy logic model is developed to predict the outcome of interactions between these factors. The model successfully simulates previous empirical findings and provides novel, testable predictions. It is argued that contrafreeloading does not contradict reinforcement theory, provided that the sensory reinforcement obtained from stimuli associated with the earned food is also taken into account. A functional explanation of why such stimuli are reinforcing, and of contrafreeloading itself, is based upon the advantage of gathering information for animals living in changing environments (i.e. an information primacy model). Animals work for earned food in order to update their estimate of a currently sub-optimal food source because, in the longer term, it may unpredictably become the optimal place to feed. Contrafreeloading is therefore a behaviour that, under natural conditions, is adaptive.

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Contrafreeloading occurs when animals work for food even though identical food is freely available; for example, a rat pressing a lever for food (i.e. 'earned' food) when the same food can easily be obtained from a dish (i.e. 'free' food) close to the lever (e.g. Jensen 1963). Contrafreeloading seems to contradict the predictions of two different theoretical frameworks: learning and motivation theory, and optimal foraging theory. According to both frameworks, animals are predicted to maximize the ratio of reward, or benefit, to effort, or cost (e.g. Hull 1943; Ferster & Skinner 1957;

Mackintosh 1974; Stephens & Krebs 1986; Krebs & Kacelnik 1991). Although working for food when the same food is freely available appears to conflict with these predictions, contrafreeloading has been demonstrated in many different species and experimental situations (Osborne 1977). In this paper we review the factors that affect the level of contrafreeloading, develop a fuzzy logic model of contrafreeloading based upon general principles that emerge from the review, and propose a functional explanation of the phenomenon.

Contrafreeloading has been demonstrated in a variety of vertebrate species (Table I), the domestic cat, *Felis domesticus*, being the only species so far showing no evidence of the phenomenon (Koffer & Coulson 1971). Contrafreeloading is most commonly studied by presenting the animal with a choice between free access to a bowl of food, and an operant task that provides response-dependent

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Table I. Species in which contrafreeloading has been found

Species	Common name	References
Betta splendens	Siamese fighting fish	Baenninger & Mattleman (1973)
Columba livia	Laboratory pigeon	e.g. Neuringer (1969)
Gallus gallus domesticus	Domestic fowl	Duncan & Hughes (1972)
Corvus brachyrhynchos	Crow	Powell (1974)
Sturnus vulgaris	Starling	Inglis & Ferguson (1986)
Rattus norvegicus	Laboratory rat	e.g. Jensen (1963)
Rattus norvegicus	Wild brown rat	Inglis & Shepherd (1994)
Rattus rattus	Wild black rat	Powell (1974)
Mus musculus	Laboratory mouse	Pallaud (1971)
Meriones unguiculatus	Gerbil	e.g. Forkman (1991)
Macaca mulatta	Rhesus macaque	Reinhardt (1994)
Macaca arctoides	Stump-tailed macaque	Anderson & Chamove (1984)
Pan troglodytes	Chimpanzee	Menzel (1991)
Homo sapiens	Children	e.g. Singh (1970)
Homo sapiens	Adults	e.g. Tarte (1981)

access to identical food, although similar results have been found using water (Taylor 1972; Knutson & Carlson 1973; Tarte et al. 1974; Robertson & Anderson 1975). The schedule of reinforcement has varied between continuous reinforcement (e.g. Jensen 1963; Neuringer 1969), fixed-ratio schedules (FR, e.g. Carder & Berkowitz 1970; Tarte & Vernon 1974) and variable interval schedules (VI, e.g. Neuringer 1970; Rachlin & Baum 1972; Bilbrey et al. 1973). Some experiments, rather than employ continuously available free food, have presented a choice between response-independent and response-dependent food (Singh 1970; Morgan 1974). Non-operant paradigms have also been employed. Animals in mazes often choose to take a long, indirect way to food rather than a shorter, direct route (e.g. Snygg 1936; Hebb & Mahut 1955; Havelka 1956; Stolz & Lott 1964; Leung et al. 1968; Jensen et al. 1970; Larson & Tarte 1976). They will also search for food (Anderson & Chamove 1984; Inglis & Ferguson 1986; Forkman 1991, 1996) or solve puzzles for food (Menzel 1991; Reinhardt 1994) rather than take freely available identical food.

The criterion for a preference in contrafreeloading studies has been defined in different ways. In his review, Osborne (1977) concluded that 'preference for a food source exists when the proportion of the total food obtained from that source exceeds 50% of the total food obtained during a session'. However, as Morgan (1974) stated, 'there is no reason to suppose that 50% represents a magic point of discontinuity

for the rat between ''preference'' and ''non-preference''.' Indeed the optimal foraging and learning paradigms predict a total preference for the free food, so that any deviation from that result has to be explained using other theories. The important questions are, first, why should the animal work at all, and second, what variables determine the strength of the contrafreeloading phenomenon?

The following review is structured around the causal factors thought to influence contrafreeloading, together with their associated explanations. Five major explanations have been proposed.
(1) Stimuli associated with food delivery from an operant dispenser become secondary reinforcers and this secondary reinforcement maintains contrafreeloading (Alferink et al. 1973).
(2) Differential exposure to the two food sources during training results in neophobia to the free food source (Mitchell & White 1977).
(3) Stimulus changes associated with the earned food are reinforcing in their own right and this sensory reinforcement maintains contrafreeloading (Osborne & Shelby 1975).
(4) Both food and information act as incentives determining the animal's choices. In seeking information the animal prefers the earned food source because it has a higher level of uncertainty. Contrafreeloading is seen either as a form of exploration (Inglis & Ferguson 1986) or a means by which the animal assesses its own abilities (Singh 1970).

(5) The behaviour required to obtain the earned food is self-reinforcing (Jensen 1963).

FACTORS AFFECTING THE LEVEL OF CONTRAFREELOADING

Prior Training

Jensen (1963) reported that when presented with a choice between bar pressing for food pellets or eating the same pellets from a dish, all but one of the 200 rats tested left the dish and worked for food at some time during the experimental trial. Furthermore, the percentage of pellets eaten that were earned by bar pressing was positively correlated with the number of rewarded presses made during training before the experimental trial. The preference for earned food therefore seemed to be a function of the habit strength formed during the training period. Subsequent experiments by Stolz & Lott (1964), Davidson (1971), Kleinman et al. (1976) and Mitchell & White (1977) supported this view. Lentz & Cohen (1980) reported the same result in pigeons, although Atnip & Hothersall (1973) and Hothersall et al. (1973) failed to find such an effect in rats.

It is possible that stimuli associated with the response-dependent food presentation during training could then act as a secondary reinforcer (e.g. Egger & Miller 1962) for contrafreeloading during test trials. Alferink et al. (1973) trained pigeons in a key pecking task and then gave them the choice of either working for food using this operant, or taking food freely from a dish. When, during testing, the hopper light was contingent upon completion of the operant task, as it was during training, responding occurred; but when the hopper light was withheld, responding ceased. However, contrary evidence was provided by Stephens et al. (1975). Rats were trained to bar press for food and then presented with a four-choice situation involving: (1) a free-food dish, (2) a non-functional lever away from the free-food dish, (3) a non-functional lever adjacent to the free-food dish and (4) a functional lever from which a food pellet was dispensed with each press. The rats overwhelmingly obtained food by bar pressing on the functional lever, despite the fact that the same auditory feedback and motor activity could be obtained at the two non-functional levers. The results of further experiments make it unlikely that the

sound and sight of the food pellet dropping into the food dish (stimuli absent from the non-functional levers in this experiment) act as secondary reinforcers (Carder & Berkowitz 1970; Singh 1970).

The effect of training on subsequent levels of contrafreeloading has been explained by Mitchell and co-workers (Mitchell et al. 1973, 1974, 1981) as neophobia towards the free-food container, since in many of the early contrafreeloading experiments, animals received operant training before the test but had no prior experience of the free-food container. Wild rats have strong neophobic responses to novel objects including food containers (e.g. Cowan 1976; Wallace & Barnett 1990), and Mitchell (1976) concluded that laboratory rats are also neophobic to some degree. Mitchell et al. (1973) found that contrafreeloading was negatively correlated with the familiarity of the free-food container.

Carder & Beckman (1975) criticized Mitchell et al.'s (1973) study, arguing that because the rats had been allowed to feed from the free-food container during training, the results were confounded with prior feeding habits. They therefore exposed one group of rats to an empty food container prior to testing whilst a second group experienced the free-food container for the first time during the choice test. If container neophobia is a major factor, the rats experiencing the free food in the familiar container should contrafreeload less than the animals obtaining free food from a novel container. The proportions of earned food in the two groups were not significantly different. However, Mitchell et al. (1981) replicated this work, and reported that rats most exposed to the free food source, but without feeding from it, did indeed show the lowest preference for earned food.

The evidence from studies designed to test the neophobia hypothesis is therefore equivocal. In addition, this hypothesis cannot account for the numerous studies where there was equal exposure to both food sources and yet contrafreeloading still occurred (Neuringer 1969; Singh 1970; Singh & Query 1971; Bilbrey et al. 1973; McLaughlin et al. 1973; Wallace et al. 1973; Morgan 1974; Osborne & Shelby 1975; Carlson & Riccio 1976; Coburn & Tarte 1976; Kopp et al. 1976; Lamal 1978; Tarte 1981; Inglis & Ferguson 1986; Rutter & Nevin 1990; Forkman 1991, 1993a, 1996; Inglis & Shepherd 1994). It also cannot explain why, in

experiments that involved training, most free feed-ing occurs at the start of a trial (Neuringer 1970; Davidson 1971; Tarte & Snyder 1972; Taylor 1972; Knutson & Carlson 1973; Mitchell et al. 1973; Robertson & Anderson 1975) since free feeding should increase over the trial, as neopho-bia towards the free-food container declined.

Convincing evidence that contrafreeloading is not solely a function of prior training comes from the many studies showing that such behaviour can be acquired and maintained despite continuous access to free food and without training in the response required (e.g. Snygg 1936; Neuringer 1969; Singh 1970; Singh & Query 1971; Baeninger & Mattleman 1973; Bilbrey et al. 1973; McLaughlin et al. 1973; Wallace et al. 1973; Coburn & Tarte 1976; Kopp et al. 1976; Inglis & Ferguson 1986; Rutter & Nevin 1990; Forkman 1993a, 1996). In addition, animals contrafreeload despite equal training on both free food and response-dependent food sources (Tarte & Snyder 1973; Osborne & Shelby 1975). Intensive pre-trial training is clearly not a necessary condition for contrafreeloading.

Deprivation Level

Tarte & Snyder (1972) reported that rats tested under 0 h or 12 h food deprivation took a smaller percentage of earned food than animals deprived for 24 h or more and suggested that contrafree-loading is caused by high levels of hunger. How-ever, subsequent studies by Morgan (1974), with rats, and Inglis & Ferguson (1986), with starlings, found that increasing hunger decreased contra-freeloading. Further evidence that high levels of contrafreeloading are not dependent upon strong deprivation comes from many studies reporting such behaviour under zero deprivation (Neuringer 1969; Singh 1970; Duncan & Hughes 1972; Bilbrey et al. 1973; McLaughlin et al. 1973; Wallace et al. 1973, Coburn & Tarte 1976; Kopp et al. 1976; Inglis & Ferguson 1986; Rutter & Nevin 1990). It is clear therefore that variables other than hunger are responsible for high levels of contrafreeloading, particularly since animals may fail to eat much of the earned food (Neuringer 1969; Mitchell et al. 1973; Wallace et al. 1973; Inglis & Shepherd 1994).

Since hunger will decline throughout the trial, within-trial changes in the proportion of food obtained by contrafreeloading should also shed light upon the effect of hunger level. As we have seen, most free feeding takes place at the begin-ning of the trial with a subsequent increase in contrafreeloading. This result supports the conclusion that contrafreeloading decreases with deprivation.

Effort Required

The relative effort involved in obtaining earned and free food is important in determining the level of contrafreeloading. Carder & Berkowitz (1970) found that rats' preference for earned food decreased from over 80% when two presses per reinforcement (i.e. FR2) were required to less than 30% when 10 presses per reinforcement (i.e. FR10) were needed. They concluded that 'as long as the work demands are not too high rats prefer earned food rather than free food'. Hothersall et al. (1973) reported no significant decrease in contrafreeloading when the response-dependent food schedule was changed from FR1 to FR2 to FR10. However, a possible explanation of this negative result lies in the fact that two of their eight rats showed negligible contrafreeloading under any schedule. The data from the remaining animals indicate a fall in contrafreeloading with increase in the FR schedule. Further evidence that increased effort reduces contrafreeloading comes from the experiments of Singh (1970), Sawisch & Denny (1973), Tarte & Vernon (1974), Lamal (1978) and Rutter & Nevin (1990).

It is not just the effort involved in obtaining the earned food that is important. Atnip & Hothersall (1973) suggested that 'free' food is not really free in many contrafreeloading studies. They noticed that their rats had to climb up the side of the free-food container and then lean down into it in order to retrieve a pellet. In other words, the effort required to obtain 'free' food could be as great, if not greater, than the effort needed to obtain earned food. Mitchell et al. (1982) tested this idea by comparing the tendency for rats to contrafree-load when the free food was placed in either a tall dish, which necessitated the animals climbing up the sides, or a short dish, which required no climbing. As predicted, the rats with the tall free-food containers showed the greater contra-freeloading. Clearly the difference in the effort required to eat at the two food sources is an important factor.

Stimulus Change

Contrafreeloading is strongly affected by stimulus changes correlated with the presentation of earned food. Alferink et al. (1973) showed that contrafreeloading by pigeons was dependent upon the operation of the food-hopper light. When key-pecking had no effect on the hopper light, contra-freeloading fell to a low level; it recovered when the hopper light contingency was reinstated. Osborne & Shelby (1975) found similar results with rats. Wallace et al. (1973) placed pigeons in experimental chambers where food was continuously available either by key-pecking or from a dish. When the key-peck produced both food and a visual stimulus, the birds made over 100 responses per session. Responding dropped to almost zero when the stimulus was made contingent on eating free food but obtaining earned food produced no stimulus change. Morgan (1974) assessed choice behaviour of rats on a concurrent schedule of reinforcement. On one side of the experimental chamber, lever presses produced a pellet every 30 s; on the other side, response-independent pellets were delivered regularly every 30 s. When a light signal was added to the response-dependent compartment the time spent working for food in that compartment increased markedly.

Such studies demonstrate that working for earned food without associated stimulus changes is not sufficient to maintain contrafreeloading in an operant situation. However, other experiments (Neuringer 1969; Duncan & Hughes 1972; Tarte et al. 1974; Osborne & Shelby 1975) show that response-produced stimulus change alone is not sufficient to maintain responding in the presence of free food. We discuss later why animals should work for their food only when the operant responses produce both food and stimulus change, and show that a specific response-dependent stimulus is not essential for contrafreeloading.

Two explanations, which are not mutually exclusive, have been proposed to explain the way in which contingent stimulus change affects con-trafreeloading (Osborne 1977). The first argues that the stimulus change becomes a secondary reinforcer after repeated pairing with food presentation during training. This explanation cannot account for the many experiments showing con-trafreeloading without training. The second explanation is that stimulus change is reinforcing in its own right so that contrafreeloading is not working

for food alone, but for food plus sensory reinforcement. The combined reinforcement is thought to be sufficient to maintain responses for earned food in the presence of free food (Osborne & Shelby 1975). There is a body of literature demonstrating that satiated animals will work solely to experience simple stimulus changes (see Kish 1966).

Sensory reinforcement theory can account for contrafreeloading without prior training since the stimulus changes should be effective from the outset. Indeed, according to this theory, training would decrease the effects of the stimulus changes because some satiation to them (Glanzer 1953) will occur during training. This prediction is supported by Tarte & Snyder (1973), who found that contrafreeloading decreased as the number of reinforced training responses increased. However, Jensen (1963) reported the opposite trend. There need be no contradiction; the conditioned reinforcement and stimulus change reinforcement theories are not mutually exclusive. The number of training trials will determine which effect dominates during the test period. With only a few or no training trials sensory reinforcement effects will dominate since there will be too few pairings of stimulus change with earned food to establish the contingent stimulus change as a strong conditioned reinforcer. As the number of training trials increases, there will be greater satiation of the sensory reinforcement effect and strengthening of the conditioned reinforcer effect.

If contrafreeloading is strongly influenced by sensory reinforcement then it should decline with increasing number and/or duration of test trials because stimulus satiation to the contingent stimulus change will occur. If secondary reinforcement is the main causal agent then the opposite should occur since repeated, long trials serve to increase the number of pairings between stimulus change and earned food thereby maintaining the contingent stimulus change as a conditioned reinforcer. There is evidence of both effects. A shift away from responding for food with repeated choice trials has been found in many studies (Duncan & Hughes 1972; Taylor 1972, 1975; Knutson & Carlson 1973; Stephens et al. 1975; Tarte & Rasmussen 1979; Mitchell et al. 1981; Nau et al. 1981; Feild et al. 1984). There have also been reports of no significant decreases in contrafreeloading over trials

(Davidson 1971; Tarte & Snyder 1973; Coburn & Tarte 1976; Kopp et al. 1976). After looking at the methodology of such studies, Tarte & Rasmussen (1979) concluded that 'rats only maintain high levels of responding following intensive training', a finding supporting the secondary reinforcement explanation. However, in the absence of training, response levels were maintained longer if the trial length was short, which supports a sensory reinforcement effect. This is because in a short trial, and for a given rate of response, there are fewer exposures to the response-contingent stimulus.

The nature of the stimulus change affects its reinforcing potential. Berlyne (1960) coined the term 'collative variables' (i.e. variables brought together for comparison) for the stimulus properties that affect exploration; under this heading he included such characteristics as novelty, surprisingness, ambiguity and incongruity. These variables are properties of an animal–environment interaction, and imply some expectancy by the subject. Increasing the strength of the collative variables can enhance the reinforcing properties of a stimulus (e.g. Dember 1956; Barnes & Baron 1961; Welker & King 1962) although it is also clear that animals avoid very novel or incongruous stimuli (e.g. Montgomery 1955; Welker 1956; Barnett 1958; Menzel 1962; Wallace & Barnett 1990). Unfortunately, experiments systematically varying the degree of contingent stimulus change and monitoring the effects on contrafreeloading have not been conducted. Osborne & Shelby (1975) have some relevant data, however. Following a condition in which no stimulus feedback was contingent upon obtaining earned food, and where there was almost no contrafreeloading, one group of rats was given an auditory stimulus paired with earned food and a second group was given a similarly contingent visual stimulus. The addition of the stimuli greatly increased and maintained contrafreeloading. When both groups later received both auditory and visual stimuli, responding was enhanced above the level maintained by either stimulus alone. This result is predicted by sensory reinforcement theory since the collative variable strength of the contingent stimulus had been increased through the combined use of stimuli in two modalities. It cannot be explained on the basis of increased secondary reinforcement since, for each group of rats, the additional stimulus was one they had never before experienced.

Environmental Uncertainty

As discussed above, the degree of sensory reinforcement provided by a stimulus is affected by such factors as its novelty, ambiguity and surprisingness (i.e. the collative variables), which provide a degree of environmental uncertainty. If such uncertainty is the crucial factor in initiating and maintaining contrafreeloading then it should be possible to observe contrafreeloading in paradigms lacking clear response-contingent stimuli, as long as some environmental uncertainty is associated with the food-gathering task.

The importance of uncertainty of food location in the initiation and maintenance of contrafreeloading was demonstrated by Havelka (1956). Rats entered a long goal box which contained eight alcoves arranged in two groups of four. In a group of alcoves near the entrance of the goal box was placed the 'constant' food dish, always in the same alcove. The other group of four alcoves was at the far end of the goalbox and the 'variable' food dish was placed in one of these alcoves, its position chosen randomly on each trial. Rats passed the constant dish, ran down the goal box, and searched the second set of alcoves for the variable dish. When the variable dish was maintained in the same alcove, the rats shifted their feeding preference to the constant dish in the alcoves nearer the goalbox entrance. Havelka concluded that 'only when the factor of "unpredictability" was withdrawn, by fixing the location of food within what had been a variable goal, did the problem-seeking rats cease to go to the variable goal position'.

Evidence that a high degree of environmental uncertainty can reduce contrafreeloading comes from the study by Forkman (1991, 1993b). Gerbils were allowed to forage between three bowls; one with sand, the second with 30 sunflower seeds mixed with sand and the third with 250 seeds mixed with sand. The animals preferred to gather seeds from the 30-seed bowl until the relative positions of the bowls in the test cage were shifted. After this, foraging on the 30-seed bowl fell markedly and the animals increased feeding from the 250-seed bowl. Gerbils are very sensitive to the spatial relationships between objects (Wilz & Bolton 1971) and moving the food bowls constituted a large environmental change.

Environmental uncertainty can be induced not only by moving the food sources but also by

hiding the food. Anderson & Chamove (1984) reported that, in the presence of grain fed ad libitum, macaques still foraged for grain hidden in litter. Inglis & Ferguson (1986) showed that starlings searched for food randomly hidden under a large number of flaps rather than take the same food freely from a dish. Forkman (1991, 1993a, 1996) found that gerbils chose to search for food in unprofitable food sources only when the food was hidden (i.e. seeds placed in sand, under lids, or on a camouflaging surface) and not when the same food was clearly visible.

Environmental uncertainty can also be induced by unexpected changes in the food itself. Inglis & Shepherd (1994) showed that wild rats would work for contaminated food that they associated with sickness and subsequently rejected, even when wholesome food was continuously available at no extra cost. Inglis & Shepherd (1994) argued that this 'enabled the animals to gather information about a rare, but very important, event, namely, the presence of dangerous food at a previously preferred and normally safe feeding site'. A similar conclusion resulted from the maze studies of Melcer & Timberlake (1985). Thirsty rats were tested in a four-arm radial maze with three water locations and one saccharin-water location. Drinking at the saccharin location was coupled with an injection of lithium chloride, which induces nausea. Although the rats quickly learned to avoid drinking the saccharin solution, the poisoned animals still continued to sample all the arms each day. In this way the rats learned rapidly to return to drink from the same location when the saccharin solution was replaced by water.

If contrafreeloading occurs in order to gain information about the position and/or quality of uncertain food patches, then it should be weak in a species whose feeding behaviour does not involve prolonged searching for unpredictable food items. The only species so far tested that showed no contrafreeloading is the domestic cat (Koffer & Coulson 1971). Every cat ate all the free food before beginning to work for it. Koffer & Coulson (1971) explained the cats' preference for free food on the basis of 'the naturalistic food-gathering habits of pigeons, rats and cats. Rats and pigeons forage, usually obtaining small amounts of food periodically, whilst cats, being predators usually obtain a large amount of food at once.' However, in the wild, small cats hunt not only by ambushing prey, but also by searching for inconspicuous prey (e.g. Sunquist & Sunquist 1991). We might therefore expect wild cats to exhibit behaviour consistent with contrafreeloading. Shepherdson et al. (1993) reported such a finding with leopard cats, *Felis bengalensis.*

Rearing Conditions

In general, animals reared under sensory deprivation explore more when faced with novel stimuli than do animals reared under sensory enriched conditions (e.g. Zimbardo & Montgomery 1957; Woods et al. 1960). This effect holds not only for early experience but also for sensory conditions imposed in adulthood (Inglis 1975; Studelska & Kemble 1979). Sensory restricted animals are less efficient at assimilating the novel test stimuli, as indicated by greater latencies to begin exploration, and slower rates of decline in exploratory behaviour (Inglis 1975). Such findings help to make sense of the results of contrafreeloading studies with rats reared under different sensory conditions.

Coburn & Tarte (1976), Morgan et al. (1975) and Davis et al. (1975) found that sensory deprived rats showed more contrafreeloading than did sensory enriched animals. Evidence of a link between exploratory behaviour and contrafreeloading comes from the study of Nau et al. (1981). Three groups of rats were reared under different sensory conditions and then tested in a novel maze as well as under the contrafreeloading paradigm. As with earlier studies, the sensory enriched group showed the least contrafreeloading. In addition, the animals showing most stimulation-seeking in the maze also exhibited the highest level of contrafreeloading.

These results can be explained on the basis that satiation to the response-dependent stimuli takes longer for sensory deprived animals than for sensory enriched animals. There is one experiment that at first sight seems to yield contrary evidence. Tarte et al. (1973) reported that both sensory enriched and sensory deprived rats chose earned food significantly less than a control group. However, they explained their results again using the contrasts between rearing conditions and testing situation for the different experimental groups. Control animals were thought to be exploring more than enriched animals owing to the greater novelty of the test situation for the former group

(Tarte et al. 1973). Large differences between the sensory conditions of rearing (Konrad & Bagshaw 1970), or long-term housing (Inglis & Freeman 1976), and test environments can inhibit normal exploratory behaviour and Tarte et al. (1973) used this effect to explain the low levels of contrafreeloading of their sensory deprived group: 'the difference in novelty for the stimulus-deprived animals was so extreme that their actions were inhibited'.

Manipulation of the Environment

Singh and co-workers (Singh 1970, 1972; Singh & Query 1971) explained their results with human subjects in terms of White's (1959) 'competence theory'. White argued that behaviour is primarily directed towards controlling and modifying the environment and that such behaviour is self-reinforcing (see also Hendrick 1943). Being able to control the environment (e.g. Kavanau 1967) is a crucial survival trait.

Contrafreeloading might be explained on this basis since lever-pressing for earned food involves greater environmental manipulation than freely taking food from a continuously available source. If this hypothesis is correct, animals should prefer to work for response-dependent food rather than take response-independent food delivered at the same rate. Singh (1970) and Morgan (1974) offered rats the choice between a compartment where they had to lever-press for a food pellet, and another compartment where a food pellet was delivered at a rate equivalent to that obtained in the other compartment. The rats worked for response-dependent food, although the strength of this behaviour differed markedly between the two studies.

The Nature of the Foraging Task

It has been suggested that contrafreeloading occurs because the performance of the operant response required to obtain earned food is reinforcing in its own right (Jensen 1963; Kacelnik 1987). Such intrinsic reinforcement has been explained in terms of innate behaviour patterns, connected or unconnected with appetitive or consummatory acts (Hogan 1967; Gardner & Gardner 1988; Hughes & Duncan 1988)

These explanations of contrafreeloading are unsatisfactory on several counts. First, a prefer-ence for earned food over free food has been found when the animals were required to make operants involving unusual behaviours that had to be acquired (e.g. Neuringer 1969). Second, contrafreeloading occurs even though the same behaviour is required to obtain food from both food sources (e.g. Havelka 1956; Forkman 1991, 1993a; Inglis & Shepherd 1994). Third, when animals are given a choice between free food and making a response that no longer produces earned food, they take the free food (e.g. Neuringer 1969; Duncan & Hughes 1972, Singh 1972), suggesting that there is no evidence of an intrinsic appeal of the behaviour itself, as shown explicitly by Forkman (1993a).

Summary

Some contrafreeloading could be a consequence of the use of experimental paradigms that involve intensive training. As a result of such training, stimuli associated with the earned food may become conditioned secondary reinforcers sufficiently strong to maintain operant responding for food in the presence of free food. In addition, training may create different strengths of neophobia towards the alternative food sources such that free feeding becomes inhibited to some degree. However, contrafreeloading also occurs in the absence of training and the more interesting problem is to explain contrafreeloading in these studies.

In addition to training, three major factors affect the level of contrafreeloading. First, contrafreeloading occurs when stimuli associated with the earned food are neither very familiar (e.g. Alferink et al. 1973; Wallace et al. 1973; Osborne & Shelby 1975) nor very novel (Tarte et al. 1973; Forkman 1991). Many studies indicate an inverted-U relationship between the level of exploratory behaviour and the strength of the collative variables associated with the experimental stimuli (for reviews see Berlyne 1960; Fowler 1965; Eisenberger 1972; Russell 1983). As there is a positive relationship between the strength of exploratory behaviour and contrafreeloading (Nau et al. 1981), it is not surprising that a similar inverted-U relationship is present in the contrafreeloading paradigm. Second, contrafreeloading declines with increasing deprivation (e.g. Neuringer 1970; Davidson 1971; Tarte & Snyder 1972; Knutson & Carlson 1973; Morgan 1974;

Inglis & Ferguson 1986). Third, an increase in the effort required to obtain earned food relative to free food reduces contrafreeloading (e.g. Carder & Berkowitz 1970; Singh 1970; Sawisch & Denny 1973; Tarte & Vernon 1974; Lamal 1978; Rutter & Nevin 1990).

A FUZZY MODEL OF CONTRAFREELOADING

Can interactions between stimulus uncertainty, effort and hunger account for the diverse findings in the contrafreeloading literature? Two major problems arise when trying to model such interactions. First, and most important, the relationships derived from the review are stated in broad qualitative terms (e.g. if the associated stimuli are familiar then negligible contrafreeloading occurs). Second, the model must be able to deal with variables that are not precise. For example, if we rank stimuli along a dimension of stimulus uncertainty we can agree that at one extreme are familiar stimuli whilst at the other extreme are novel stimuli. However, there is no clear boundary between these categories. In between are unfamiliar stimuli having both novel and familiar features, and these stimuli may trigger, to different degrees, relationships associated with both the novel and familiar categories. A simple way to model multiple, qualitative, relationships between variables whose factor levels overlap is to use fuzzy logic. This is a mathematical theory of inference that deals with ambiguous concepts (e.g. Russell 1923; Black 1937; Zadeh 1965; Zadeh et al. 1975; Gaines 1976; Kosko 1994). We have developed a fuzzy logic model to see whether the empirical results discussed in our review can be explained by simple rules determining the interactions between stimulus uncertainty, hunger and effort. The model also provides novel and testable predictions.

Construction of the Model

The model, developed in CubiCalc (HyperLogic 1993), uses three input variables, Hunger, Stimulus and Effort. Each variable is composed of a number of fuzzy sets or 'adjectives' (see below). Hunger is an index of the level of food deprivation at the start of the experimental trial. Stimulus measures the degree of uncertainty (i.e. collative-

variable strength) created by stimuli associated with the earned food. Effort reflects the work required to obtain earned food relative to that needed to obtain free food. Figure 1 shows the adjectives that describe these variables. Each variable graph (see Fig. 1) comprises the *X*-axis along which the level of Hunger, Stimulus or Effort is measured on an arbitrary scale of 0 to 10; and the *Y*-axis, always scaled between 0 and 1, which represents the activation weight assigned to any rule (see below) that uses that particular adjective. The *Y* value indicates the degree of membership of a particular *X* value to the various fuzzy sets. For example, the value 5 of the Stimulus variable belongs 100% to the fuzzy set Moderate and therefore rules containing the adjective Moderate will be maximally activated. A Stimulus value of 3 belongs only 60% to the fuzzy set Moderate and hence rules containing the adjective Moderate will have an activation weight of 0.60. In addition, however, a Stimulus value of 3 also belongs 40% to the fuzzy set Low and therefore rules containing the adjective Low will have an activation weight of 0.40. This result stems from the degree of overlap between the fuzzy adjectives, Low and Moderate. The fuzzy logic model works by activating all rules simultaneously; however, many will contain adjectives with zero activation and hence will not contribute to the output.

The activation weights that result from a given value of a variable will depend upon the nature of the fuzzy sets that comprise the adjectives of that variable. In particular, the positions of maximum activation along the *X*-axis, the degree of overlap between adjectives, and the shape of each adjective are important parameters. Often these parameters can be set using experimental data. Since data are not available for this model the most conservative assumptions have been used instead. The number of adjectives per variable is the minimum necessary to accommodate the relationships derived from the review (see below). The positions of the points of maximal activation have been placed at the extremes of the *X*-axes and equally spaced between (see Fig. 1). The degree of overlap between adjectives is such that the activation weight of a particular adjective becomes zero at the point of maximal activation weight of the adjacent adjective (see Fig. 1). This means that, for example, when the adjective Low of the variable Hunger is maximally activated, the activation of High is zero,
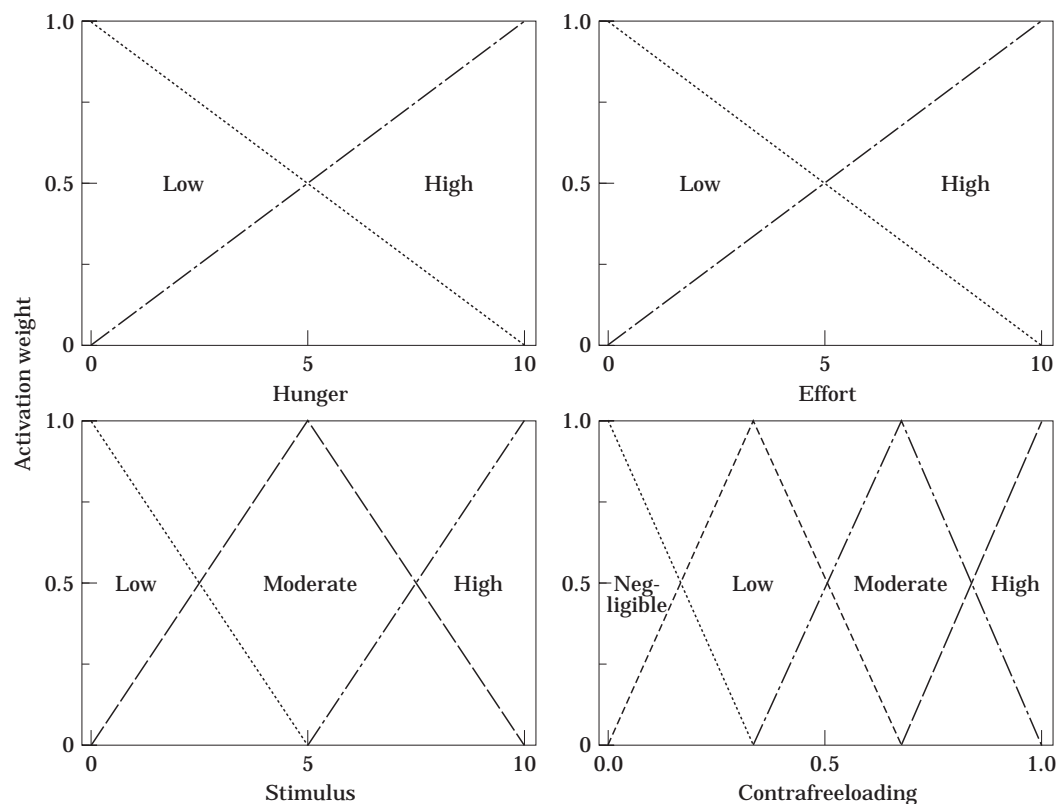
Figure 1. Shapes of the fuzzy sets, or adjectives, that make up the input variables Stimulus, Hunger and Effort, and the output variable Contrafreeloading. The various types of line indicate the boundaries of the sets. See text for details.

i.e. an animal cannot be maximally satiated and partially hungry at the same time. The model also makes the simplest assumption that there is a linear decline in activation weight away from the point of maximal activation (see Fig. 1). It might be argued that a fuzzy set based upon a normal distribution, peaking at the position of maximal activation, would be a more realistic shape. We also constructed the model using normal distribution functions for the adjective shapes but the output differed little from that obtained using linear functions. We used linear functions to obtain the results presented in this paper.

As already mentioned, the number of adjectives per variable is the minimum required in order to model the relationships derived from the review. The inverted-U relationship between the strength of the collative variables of the associated stimuli, and the level of contrafreeloading, requires that

Stimulus has a minimum of three adjectives: these have been called Low, Moderate and High. When Low is maximally activated the collative-variable strength is minimal (i.e. the stimuli are very familiar) and positive sensory reinforcement is negligible. When High is maximally activated the collative-variable strength is greatest (i.e. the stimuli are very novel) and positive sensory reinforcement is again negligible. Equidistant between these two points is the point of maximal activation of the fuzzy set Moderate where positive sensory reinforcement is greatest (Fig. 1). Contrafreeloading decreases with increases in hunger or effort and, therefore, Hunger and Effort each require a minimum of just two adjectives: these have been called Low and High for both variables. When the fuzzy set Low of Hunger is maximally activated, the animal is satiated. When High is maximally activated the animal is maximally hungry. Maximal activation of the Low fuzzy set of Effort

means that there is little difference in effort between obtaining earned and free food. When High is maximally activated, obtaining earned food requires a great deal more effort than taking the free food. The points of maximal activation for the adjectives are simply positioned at the ends of the Hunger and Effort scales (Fig. 1).

There is one output variable, Contrafreeloading, which is scaled between 0 and 1, and represents the proportion of contrafreeloading in relation to free feeding. To model the relationships already described between the three factors and the level of contrafreeloading, Contrafreeloading needs a minimum of four adjectives. One is required to describe the absence of contrafreeloading when the associated stimuli are very familiar or very novel. Contrafreeloading occurs with intermediate stimuli and, as the strength of it depends upon the degrees of both hunger and effort involved, there may logically be three levels of contrafreeloading. Least contrafreeloading occurs when there are high levels of both hunger and effort. Intermediate levels of contrafreeloading occur when the level of hunger is low and that of effort is high, or vice versa. Contrafreeloading is highest when the levels of both hunger and effort are low. In order of increasing contrafreeloading, the four adjectives required have been called Negligible, Low, Moderate and High. As with the other variables, the points of maximum activation weight are equally spaced along the Contrafreeloading dimension (see Fig. 1).

The model uses rules that determine the outcome of all interactions between the adjectives of Stimulus, Hunger and Effort in terms of the resulting four adjectives of Contrafreeloading. These rules formalize the qualitative relationships derived from the literature review and logically specify how the four levels of Contrafreeloading can be obtained.

(1) If Stimulus is Low then Contrafreeloading is Negligible.
(2) If Stimulus is Moderate and Hunger is Low and Effort is Low then Contrafreeloading is High.
(3) If Stimulus is Moderate and Hunger is Low and Effort is High then Contrafreeloading is Moderate.
(4) If Stimulus is Moderate and Hunger is High and Effort is Low then Contrafreeloading is Moderate.
(5) If Stimulus is Moderate and Hunger is High and Effort is High then Contrafreeloading is Low.
(6) If Stimulus is High then Contrafreeloading is Negligible.

When more than one rule has non-zero activation, the separate responses from each are combined to produce a single value of Contrafreeloading. To compute an output for a rule, the model uses the current activation weight of the rule as a multiplier to scale the adjective of the output variable. This method consists of changing the height of the peak of the output adjective whilst retaining its general shape (see Fig. 2). Thus the scaled output from a rule is a fuzzy set that specifies the degree to which each possible output value is a member of the response specified by the rule. The model, however, has rules containing more than one input variable. The system computes the activation weights separately for each of the input variables specified and then combines them to give a composite activation weight for the relevant output set. When rules contain 'and' (as in rules 2–5) the minimum of the activation weights becomes the activation weight of the rule. (If a rule contained 'or' between different variables then the maximum of the activation weights would become the activation weight of that rule.) The result of the activation of a rule is a scaled fuzzy set, or adjective, of the output variable.

When two or more rules are activated, two or more adjectives of Contrafreeloading will result. The model combines these adjectives by adding them as functions to create a new shape for the combined fuzzy set (Fig. 2). A single numeric output value is then obtained by extracting the numeric value of the centroid (i.e. the centre of gravity, see Fig. 2) of this new fuzzy set. The result of the operation of the fuzzy logic system is therefore a single numeric value for Contrafreeloading.

The model is designed to plot changes in contrafreeloading over time, time being represented by iterations of the model. The model has three main parts (pre-processing, fuzzy system and post-processing) which operate on each iteration. In pre-processing, the values of Hunger and Stimulus are calculated for that iteration. The value of Effort remains constant since we decided to ignore any decrease in effort that might occur
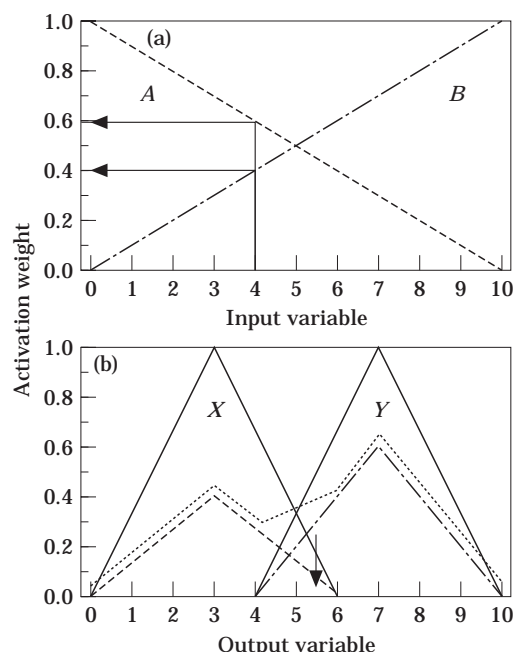
Figure 2. An example of the operation of a simple fuzzy system. The Input variable has two adjectives, *A* and *B* (see (a)). Both span the whole range of the variable but *A* has maximum activation at 0 and *B* has maximum activation at 10. The Output variable also has two adjectives, *X* and *Y* (see (b)). *X* spans the range 0–6 with maximum activation at 3, and *Y* spans the range 4–10 with maximum activation at 7. The system has two rules; rule 1: if Input is *A* then Output is *Y*, and rule 2: if Input is *B* then Output is *X*. Consider an Input value of 4. This will result in activation weights of 0.6 for *A* and of 0.4 for *B* (see (a)). Hence rule 1 will have an activation of 0.6 and rule 2 of 0.4. As a result, the Output adjective *Y* will have a peak activation of 0.6 and adjective *X* a peak activation of 0.4 (see (b)). These output sets are added (as indicated in the dotted line of (b)) to produce a combined fuzzy set. The centroid value (or centre of gravity) of this new set (i.e. a value of 5.4, as indicated by the arrow in (b)) is then calculated. This fuzzy system, therefore, produces an Output value of 5.4 for an Input value of 4.

through increasing skill. This would be small in proportion to the magnitude of the differences in time and energy required to obtain food from the response-dependent and response-independent food sources. After the values of Hunger and Stimulus have been calculated, they are, together with the value of Effort, acted upon by the rules of the fuzzy system to produce a value

of Contrafreeloading. In post-processing, the amount of free food taken is calculated as $((1 - \text{Contrafreeloading}) \times C_f)$ where C_f is a constant representing the amount of food that could be obtained if the animal took only free food. Similarly the amount of earned food is given by $(\text{Contrafreeloading} \times C_e)$ where C_e is a constant representing the amount of food that could be obtained if the animal took only earned food. By the nature of the contrafreeloading paradigm, $C_f > C_e$. The degree of stimulus satiation to the stimulus associated with the response-dependent food source is given by $(\text{Contrafreeloading} \times C_s)$ where C_s is a constant representing the degree of stimulus satiation that would accrue if the animal had shown only contrafreeloading behaviour. The total amount of food obtained is simply the sum of the amounts of free food and earned food. This value is fed into pre-processing and subtracted from the current value of Hunger to get the new value for the next iteration. Similarly, the amount of stimulus satiation is fed back into pre-processing and subtracted from Stimulus to get a new value for the next iteration.

Output of the Model

The model uses three constants (i.e. C_f, C_e and C_s) and it is important to see how sensitive the output from the model is to changes in the values of these constants. In the following simulations the initial input variables were: Stimulus=5, Hunger=5 and Effort=5 (i.e. all set to the mid-range values). A trial was defined as 10 iterations and Hunger was reset to 5 between trials. The value of Stimulus was not reset between trials although in practice there might be some dishabituation towards the response-contingent stimuli with long inter-trial intervals. This can be modelled by increasing Stimulus between trials, which has the effect of increasing Contrafreeloading to a degree dependent upon the size of the inter-trial recovery.

Figure 3 shows examples of the changes in the mean level of Contrafreeloading per trial that occur with variation in C_f and C_e. It can be seen that the model is robust to large variations in these constants. Robertson & Anderson (1975) reported no significant effects of magnitude of the earned food reward (i.e. equivalent to changes in the C_f to C_e ratio) on the level of contrafreeloading. However, small changes in C_s have large effects on Contrafreeloading (see Fig.
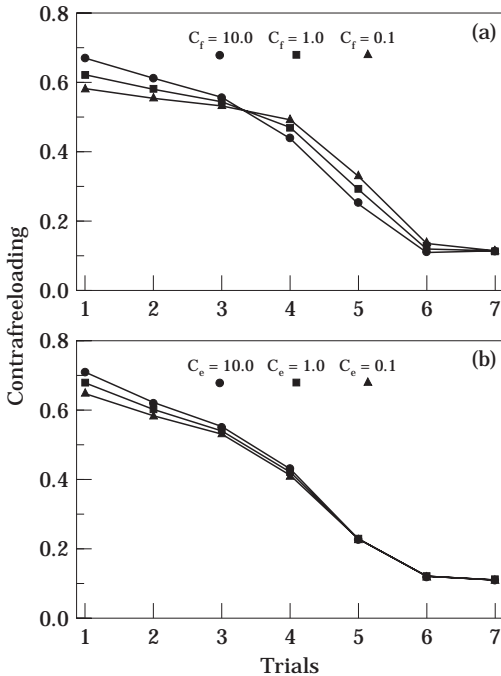
Figure 3. The effects on Contrafreeloading of changes in C_f and C_e (where the former is a constant representing the amount of food that could be obtained if the animal took only free food, and the latter a constant representing the amount of food that is available if the animal took only earned food). The initial conditions are Stimulus=5, Hunger=5, Effort=5, and C_s=0.2 (i.e. a constant representing the degree of stimulus satiation that would occur if the animal shows only contrafreeloading behaviour). There are 10 iterations of the model per trial and Hunger is reset to 5 between trials. In (a) C_e=0.01 and C_f is varied; in (b) C_f=10.0 and C_e is varied.

4): decreasing C_s prolongs Contrafreeloading. C_s represents the maximum rate at which stimulus satiation occurs. It would be a function of both the experimental procedure (i.e. how long the stimuli are encountered per unit time of contrafreeloading), and the efficiency of the animal's stimulus satiation processes, which will vary with such factors as previous sensory experience. Note that although Contrafreeloading is scaled between 0 and 1, the minimum value that emerges from the model is 0.11. This is because the model works using the centroid values of the fuzzy sets of the output variable. Hence the lowest value of Contrafreeloading is the centroid value of the fuzzy set of the adjective Negligible
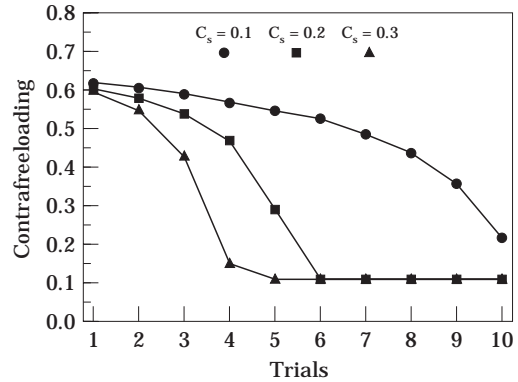

Figure 4. The effects on Contrafreeloading of changes in C_s when the initial conditions are: Stimulus=5, Hunger=5 and Effort=5. There are 10 iterations of the model per trial and Hunger is reset to 5 between trials. The other constants in the model are C_f=1.0 and C_e=0.1 (see Fig. 3).

when this has maximum activation weight. This value is approximately 0.11. Similarly the highest possible value of Contrafreeloading is approximately 0.89 which is the centroid value of the fuzzy set produced when High has maximum activation weight.

Although we cannot relate the absolute values of Contrafreeloading produced by the model to empirical data, we can examine how well the model simulates observed qualitative effects. For example, major changes between trials in the stimuli associated with the earned food produce a drop in contrafreeloading (Forkman 1991). Increasing Stimulus to a high value between trials similarly results in a drop in Contrafreeloading. However, such an effect is expected since rule 6 of the model specifies that stimuli with high collative-variable strength inhibit contrafreeloading. It is more valuable to see how well the model simulates observed effects that are not directly implied by the rules used in the model. For example, many studies have found that most free feeding takes place at the begining of a trial, with a subsequent increase in contrafreeloading. Over a wide range of initial Stimulus, Hunger and Effort conditions, the model similarly indicates an increase in Contrafreeloading throughout the trial. This finding is not obviously implied by the rules of the model. If simulations of known phenomena are successful we can then place more confidence in the novel predictions of the model.
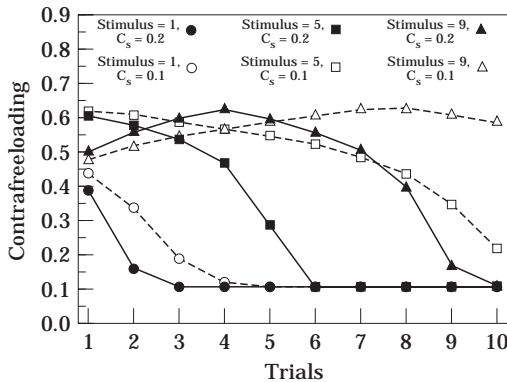
Figure 5. The effects on Contrafreeloading of changes in Stimulus. The initial conditions are Hunger=5 and Effort=5. There are 10 iterations of the model per trial and Hunger is reset to 5 between trials. The constants used are C_f=1.0, C_e=0.1 and C_s=0.1 or 0.2 (see Fig. 3).

Initially we conducted simulations to examine the effects of variations in the three input variables. For the simulations presented here, C_f=1.0 and C_e=0.1, and two values of C_s have been used, 0.2 and 0.1 because of the sensitivity of contrafreeloading to this constant. A trial was defined as 10 iterations. The level of Contrafreeloading is very sensitive to changes in the initial value of Stimulus (see Fig. 5). When Stimulus=1 (i.e. the stimulus is familiar), Contrafreeloading falls to the baseline after only three or four trials. When Stimulus=5 (i.e. the point at which sensory reinforcement is maximal) the initial level of Contrafreeloading is greater than when Stimulus=9 (i.e. the stimulus is novel). At high values of Stimulus, rule 6 has the greatest activation weight and this rule specifies that stimuli with high collative-variable strength produce negligible contrafreeloading. Nevertheless some stimulus satiation will occur because other rules are active to a small degree, and hence the value of Stimulus will decline. As the decline proceeds, the activation weight of rule 6 will also decline and the activation weights of the other rules increase so that Contrafreeloading also increases. As shown in Fig. 5, a cross-over occurs between the two curves for Stimulus=5 and Stimulus=9; the trial on which this occurs varies with the value of C_s. Stimulus satiation over the initial trials reduces Contrafreeloading when Stimulus=5, but increases it when Stimulus=9.

These simulations provide results congruent with the effects of rearing environments on contrafreeloading. As already discussed, animals reared under sensory deprivation conditions show more contrafreeloading than animals reared in sensory enriched environments because deprived animals take longer to habituate to the response-dependent stimuli. This could be because these stimuli are more novel for the sensory deprived animals, and/or because sensory deprived animals are less efficient at assimilating novel sensory input. As Fig. 5 shows, the model predicts that Contrafreeloading will be most prolonged at high values of Stimulus (i.e. when the stimuli are most novel), and at low levels of C_s (i.e. when the rate of stimulus satiation is low). Tarte et al. (1973) produced results seemingly at odds with the other studies. They reported that both sensory deprived rats and sensory enriched rats showed lower levels of contrafreeloading than those reared under normal laboratory conditions. Figure 5 shows that such an effect is also predicted by the model: the sensory deprivation group (i.e. Stimulus=9) shows less Contrafreeloading than the normal group (i.e. Stimulus=5), but only over the first few trials. The study of Tarte et al. (1973) did in fact measure contrafreeloading over just two trials.

Similar cross-over effects are evident in the simulations involving changes in Hunger and Effort (see Fig. 6). Over the initial trials, increasing Hunger or Effort decreases Contrafreeloading as expected from the rules used. However, less contrafreeloading means less stimulus satiation and hence a slower decline in contrafreeloading over trials. As a result, after many trials have been completed, Contrafreeloading at high levels of Hunger or Effort is greater than at low levels. The model also predicts that the effects of Effort become more important as Hunger increases (see Fig. 7). Unfortunately no studies have examined these predictions; they would be an important test of the model.

After examining the methodology of contrafreeloading studies, Tarte & Rasmussen (1979) concluded that, in the absence of intensive training, contrafreeloading was maintained longer if the trial length was short. By varying the number of iterations used to define a trial, the model can simulate the effect of trial length. Figure 8 shows that the model produces results in agreement with Tarte & Rasmussen's conclusion.
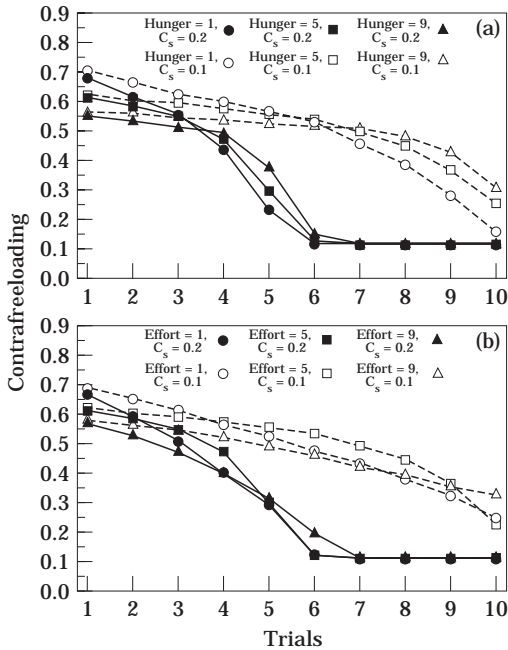
Figure 8. The effects of trial length on Contrafreeloading. The initial conditions are Stimulus=5, Hunger=5 and Effort=5. The constants used are C_f=1.0, C_e=0.1, and C_s=0.2 or 0.1 (see Fig. 3). The number of iterations of the model per trial were either 5 (trial=5), 10 (trial=10), or 20 (trial=20). Hunger was reset to 5 between trials.

Figure 6. The effects on Contrafreeloading of changes in Hunger or Effort. There are 10 iterations of the model per trial and Hunger is reset to its initial value between trials. The constants used are C_f=1.0, C_e=0.1 and C_s=0.1 or 0.2 (see Fig. 3). (a) shows the effect of variation in Hunger (with the initial values, Stimulus=5 and Effort=5); (b) the effect of variation in Effort (with the initial values, Stimulus=5 and Hunger=5).
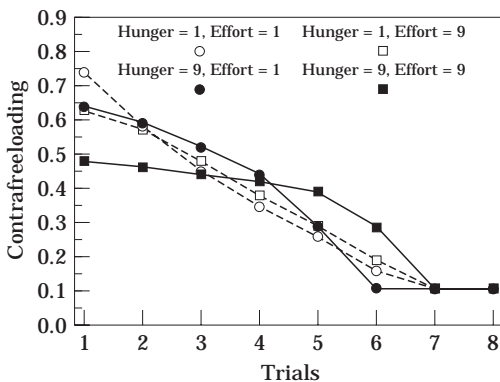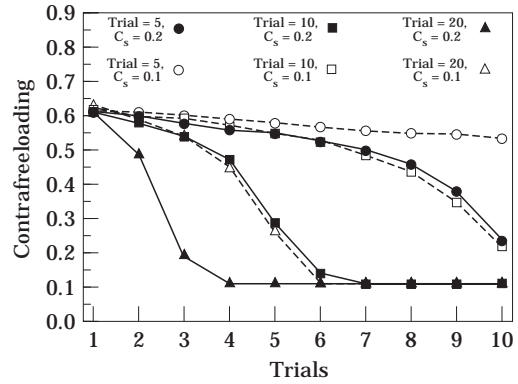

Figure 7. The effects on Contrafreeloading of the interaction between Hunger and Effort. The initial value of Stimulus=5, there are 10 iterations of the model per trial, and Hunger is reset to its initial value between trials. The constants used are C_f=1.0, C_e=0.1 and C_s=0.2 (see Fig. 3).

The ability of this simple fuzzy logic model to simulate the observed effects on contrafreeloading of factors such as trial length and rearing conditions supports the argument that the relationships derived from the literature review are indeed important in explaining variation in contrafreeloading. The results of the simulations indicate that interactions between: (1) the degree of uncertainty created by stimuli associated with the earned food source, (2) the level of hunger, and (3) the relative effort required to obtain earned as opposed to free food can account for much of the wide range of results published in the contrafreeloading literature. The model has also produced a number of novel and testable predictions. Fuzzy, rule-based models could be useful for simulating many of the more cognitive aspects of animal behaviour. The superb work of Holland et al. (1987) has shown in detail how inductive models of the physical and social environment can be created by rule-based systems.

EXPLANATIONS OF CONTRAFREELOADING

Causal Explanations

Does contrafreeloading contradict the basic tenet that animals try to maximize their reinforcement/effort ratio? Yes it does, but only if reinforcement is equated with the food eaten.

As Osborne (1977) argued, it is not only the reinforcement of the food itself but also the reinforcing effects of stimuli associated with the presentation of the food, both earned and free, that have to be taken into account. When the consequences of working for food or taking free food are made more equally reinforcing, by equating the stimulus changes associated with each, very little contrafreeloading is found. This is in contrast to the greater degree of contrafreeloading found when stimulus change is greater for the earned food. There have been two explanations for why, in the absence of training, working for food plus stimulus change is preferred over taking free food without stimulus change. First, Osborne & Shelby (1975) have suggested that animals respond for food plus stimulus change because the reinforcement provided by the stimulus change is increased in the presence of other, more potent, primary reinforcers, i.e. food. The heightened sensory reinforcement effects, added to the primary reinforcement effects of response-dependent food, are such that the total reinforcement obtained by responding is sufficient to maintain responding when free food is available. Second, the information primacy approach of Woodworth (1958) and Inglis (1983, 1987) argues that information gathering is vital, and is a function of most behaviour patterns, for animals living in changing environments. Only when need states become intense enough do animals concentrate exclusively upon fulfilling those needs. Animals work for food both in order to obtain food and to reduce uncertainty associated with the source of food.

Since food rewards become more potent primary reinforcers as deprivation increases, Osborne & Shelby's (1975) model predicts that the reinforcing value of the response-contingent stimulus change, and hence contrafreeloading, will also increase with deprivation. The information primacy model predicts the opposite, since a more intense need state disrupts information-gathering behaviour and triggers behaviour directed to reducing the need state. Preference for free food should therefore increase with deprivation. Contrafreeloading decreases with deprivation, supporting the information primacy explanation.

Functional Explanations

There are at least three functional reasons why information gathering is vital for animals living in changing environments. First, animals construct cognitive models that enable spatial and temporal predictions, or 'expectancies', to be made about the environment (e.g. Tolman 1932, 1948), and selection will favour the construction of models that produce the most accurate expectancies. The causal nature of the environment permits only stochastic predictions (Tolman & Brunswik 1935), and such expectancies can have strength in two ways: first, in the sense that stimulus A will follow stimulus B with a certain probability; and second, an expectancy can have strength in that it is strongly held, even if the expected probabilty of the stimulus B consequence is very low (Tolman 1959). This second aspect, the 'confidence rating' (Inglis 1983, 1987), is determined largely by the variance of the animal's past experience. Gathering information about stimuli that either are not associated with any current expectancies, or are associated with expectancies having low confidence ratings, will increase the reliability of the model. Behaviour is a result of a continual compromise between satisfying the current physiological needs and the need to maintain an accurate and reliable cognitive model.

Second, cognitive models must use induction, and reasoning from particular instances to general conclusions cannot be made on the basis of a series of unique stimuli. For an instance to be successfully categorized into its proper class, some indication is needed about the degree of variability usually pertaining among examples of those classes. As Holland et al. (1987) argued, 'induction is guided by background knowledge about the variability of classes of objects and events. It follows that a major goal of inductive systems is to learn about the variability of the environment.'

Third, attempting to maximize the reward:effort ratio in an uncertain environment can be viewed as a 'hill climbing' optimization problem, i.e. searching for the highest, or optimal, peak. If the animal invariably tries to maximize this ratio (i.e. it only moves uphill), it runs the risk of being stuck at a local optimum that is globally suboptimal since, once at a local optimum, any search for a higher peak must initially necessitate a movement downhill (i.e. a decrease in the reward:effort ratio). This is why optimization algorithms include a random element (e.g. Harth & Tzanakou 1974). Adding noise tends to shake the system from local optima and increases the

probability that the true optimal solution will be found (e.g. Hinton & Sejnowski 1986). Exploratory behaviour performs the same function more efficiently than random movements (e.g. Stadden 1983) because the animal does not run the risk of wasting time and energy investigating areas already well known to it; rather it concentrates on unfamiliar locations that may provide better options. De Valois (1954) found that increasing thirst reduced behavioural variability in a complex maze, and that only the less thirsty animals (i.e. those that had exhibited exploratory behaviour) subsequently discovered a shorter route to the goal box following changes to the maze. Optimal behaviour in the long term depended upon suboptimal behaviour in the short term.

The continual gathering of information therefore has adaptive value, particularly in rapidly changing physical and social environments. Many animals continually check features in their home range (e.g. Barnett & Cowan 1976; Barnett et al. 1978) and this behaviour is little affected by food reward or deprivation (e.g. Fitzgerald et al. 1985; Cowan 1977). The latent learning phenomenon (e.g. Thistlethwaite 1951) demonstrates that animals learn from their exploratory behaviour, even though it goes unrewarded. Applying the information primacy approach to contrafreeloading, we conclude that animals work for earned food partly for the food itself, and partly to improve and update their estimate of the profitability of an uncertain food source that may unpredictably become the optimal place to feed.

Work on sampling and foraging in an uncertain environment supports this interpretation. Models have been developed that predict the optimal level of sampling (i.e. the level that maximizes intake rate) in conditions where food patch profitabilities are unknown but remain stable over time, and where they fluctuate unpredictably over time between known states (Stephens & Krebs 1986; Stephens 1993). In nature, however, profitabilies will often fluctuate unpredictably both in time and amount. Consequently, animals are expected to sample not only in order to solve the kind of problems described by such models, but also to judge whether profitabilities have changed in some way that is less readily predicted by past experience (see also Houston et al. 1982). In accordance with this hypothesis, empirical tests of such models often find that animals sample more than predicted (Krebs et al. 1978; Lima 1984; Plowright & Plowright 1987; Tamm 1987; Shettleworth et al. 1988). In addition, runs of bad luck on a patch can result in animals leaving, when the predicted optimal policy is to continue. This suggests a judgement by the animal that the long-term profitability of the patch has diminished, rather than that there has been an unlucky streak in a stable stochastic state (Krebs et al. 1978; McNamara & Houston 1980; Shettleworth et al. 1988). Such work supports the view that animals sample from the earned food in contrafreeloading experiments in order to update their knowledge of the profitability of this less certain food source.

If there is a trade-off between maximally efficient foraging and information gathering, why has it generally been reported that animals forage where it is easiest to obtain food (e.g. Krebs & McCleery 1984)? An answer lies in the experimental protocols commonly used, which minimize the expression of information-gathering behaviour (Forkman 1991). First, animals are often deprived to a degree that ensures near maximum foraging efficiency. For example, Smith & Dawkins (1971) stated that 'an important factor in these experiments is that there is pressure on the tits to maximize their hunting efficiency, since each trial is preceded and followed by periods of food deprivation.' Kacelnik (1987) admitted 'it is indeed a commonly observed fact that energy-maximising models work better when the animals are hungrier' (see also Rechten et al. 1983). Second, test trials are often short (e.g. Smith & Sweatman 1974) which means that hunger level remains high and that the trial is terminated before the animal has begun markedly to vary its behaviour as a result of satiation.

Forkman (1996) investigated the relative merits of patch choice foraging theory and information primacy theory. Gerbils could forage from either a food source with easily accessible food or from a food source requiring a lot more work. When the amount of food available at each source could be immediately assessed with no effort (because there was negligible environmental uncertainty) the animals preferred the most profitable food source, in accordance with both the competing theories. However, when uncertainty was associated with the least profitable food source (i.e. the food was

hidden under lids, or was camouflaged), the animals chose this source of food, a result predicted by information primacy theory but not by patch choice models.

CONCLUSION

Contrafreeloading has often been ignored because it appeared to contradict the basic tenets of prevailing theory. This is, however, a reason for investigating rather than ignoring it. The common assumption has been that maximally efficient reduction of need in the short term largely determines behaviour. Contrafreeloading casts doubt on this assumption. Instead we suggest that behaviour is guided by the need to create as reliable a cognitive model of the environment as possible, since this greatly enhances survival in the longer term. As Shepherdson et al. (1993) argued 'information gathering is integral to all the classic motivational systems (e.g. thirst, hunger, sex). The information primacy model provides a useful umbrella under which these other motivational systems can be better understood.'

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REFERENCES

Alferink, L. A., Crossman, E. K. & Cheney, C. D. 1973. Control of responding by a conditioned reinforcer in the presence of free food. *Anim. Learn. Behav.*, **1**, 38–40.

Anderson, J. R. & Chamove, A. S. 1984. Allowing captive primates to forage. In: *Standards in Laboratory Animals Management (Part 2)*, pp. 253–256. Potters Bar, UK: Universities Federation of Animal Welfare.

Atnip, G. & Hothersall, D. 1973. The preference of albino rats for free or response-produced food. *Bull. Psychonom. Sci.*, **2**, 153–154.

Baenninger, R. & Mattleman, R. A. 1973. Visual reinforcement: operant acquisition in the presence of a free mirror. *Anim. Learn. Behav.*, **1**, 302–306.

Barnes, G. W. & Baron, A. 1961. Stimulus complexity and sensory reinforcement. *J. comp. physiol. Psychol.*, **54**, 466–469.

Barnet, S. A. 1958. Experiments on 'neophobia' in wild and laboratory rats. *Br. J. Psychol.*, **4**, 195–201.

Barnett, S. A. & Cowan, P. E. 1976. Activity, exploration, curiosity and fear: an ethological study. *Interdiscip. Sci. Rev.*, **1**, 43–62.

Barnett, S. A., Dickson, R. G., Marples, T. G. & Radha, E. 1978. Sequences of feeding, sampling and exploration by wild and laboratory rats. *Behav. Proc.*, **3**, 29–43.

Berlyne, D. E. 1960. *Conflict, Arousal and Curiosity.* New York: McGraw-Hill.

Bilbrey, J. L., Patterson, D. D. & Winokur, S. 1973. Maintenance and autoshaping of key pecking in undeprived pigeons. *Bull Psychonom. Sci*, **2**, 394–396.

Black, M. 1937. Vagueness. *Philosophy Sci.*, **4**, 427–455.

Carder, B. & Beckman, G. C. 1975. Limitations of 'container neophobia' as an explanation of rats responding for food in the presence of free food. *Behav. Biol.*, **14**, 109–113.

Carder, B. & Berkowitz, K. I. 1970. Rats preference for earned in comparison with free food. *Science*, **167**, 1273–1274.

Carlson, C. W. & Riccio, D. C. 1976. Experience with the reinforcer and the preference for earned rather than free reinforcers in rats. *Anim. Learn. Behav.*, **4**, 269–272.

Coburn, J. F. & Tarte, R. D. 1976. The effect of rearing environment on the contrafreeloading phenomenon in rats. *J. exp. Analysis Behav.*, **26**, 289–294.

Cowan, P. E. 1976. The new object reaction of *Rattus rattus*: the relative importance of various cues. *Behav. Biol.*, **16**, 31–44.

Cowan, P. E. 1977. Systematic patrolling and orderly behaviour of rats during recovery from deprivation. *Anim. Behav.*, **25**, 171–184.

Davidson, A. G. 1971. Factors affecting keypress responding by rats in the presence of free food. *Psychonom. Sci.*, **24**, 135–137.

Davis, S. F., Beighley, B. G., Libretto, J. S., Mollenhour, M. J. & Prytula, R. E. 1975. Contrafreeloading as a function of early environmental conditions. *Bull. Psychonom. Soc.*, **65**, 95–97.

Dember, W. N. 1956. Response by the rat to environmental change. *J. comp. physiol. Psychol.*, **49**, 93–95.

De Valois, R. L. 1954. The relation of different levels and kinds of motivation to variability of behaviour. *J. exp. Psychol.*, **47**, 392–398.

Duncan, I. J. & Hughes, B. O. 1972. Free and operant feeding in domestic fowls. *Anim. Behav.*, **20**, 775–777.

Egger, M. D. & Miller, N. E. 1962. Secondary reinforcement in rats as a function of the stimulus. *J. exp. Psychol.*, **64**, 97–104.

Eisenberger, R. 1972. Explanations of rewards that do not reduce tissue needs. *Psychol. Bull*, **77**, 319–339.

Feild, C. L., Kasper, S. & Mitchell, D. 1984. Effort and contrafreeloading. *Bull. Psychonom. Soc.*, **22**, 147–150.

Ferster, C. B. & Skinner, B. F. 1957. *Schedules of Reinforcement.* New York: Appleton-Century-Croft.

Fitzgerald, R. E., Isler, R., Rosenberg, E., Oettinger, R. & Battig, K. 1985. Maze patrolling by rats with and without food reward. *Anim. Learn. Behav.*, **13,** 451–462.

Forkman, B. 1991. Some problems with current patch-choice theory: a study on the Mongolian gerbil. *Behaviour*, **117,** 243–254.

Forkman, B. 1993a. Self-reinforced behaviour does not explain contra-freeloading in the Mongolian gerbil. *Ethology*, **94,** 109–112.

Forkman, B. 1993b. 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.

Fowler, H. 1965. *Curiosity and Exploratory Behavior.* New York: Macmillan.

Gaines, B. R. 1976. Foundations of fuzzy reasoning. *Int. J. Man-Machine Studies*, **8,** 623–668.

Gardner, R. A. & Gardner, B. T. 1988. Feed forward versus feed backwards : an ethological alternative to the law of effect. *Behav. Brain. Sci.*, **11,** 429–493.

Glanzer, M. 1953. Stimulus satiation: an explanation of spontaneous alternation and related phenomena. *Psychol. Rev.*, **60,** 257–268.

Harth, E. & Tzanakou, E. 1974. Alopex: a stochastic method for determining visual receptive fields. *Vision Res.*, **14,** 1475.

Havelka, J. 1956. Problem-seeking behaviour in rats. *Can. J. Psychol.*, **10,** 91–97.

Hebb, D. O. & Mahut, H. 1955. Motivation et recherche du chargement perceptif chez le rat et chez l'homme. *J. Psychol. norm. path.*, **48,** 209–221.

Hendrick, I. 1943. The discussion of the 'instinct to master'. *Psychoanal. Q.*, **11,** 243–266.

Hinton, G. E. & Sejnowski, T. J. 1986. *Parallel Distributed Processing.* Cambridge, Massachusetts: MIT Press.

Hogan, J. A. 1967. Fighting and reinforcement in the Siamese fighting fish (*Betta splendens*). *J. comp. physiol. Psychol.*, **64,** 356–359.

Holland, J. H., Holyoak, K. J., Nisbett, R. E. & Thagard, P. R. 1987. *Induction.* Cambridge, Massachusetts: MIT Press.

Hothersall, D., Huey, D. & Thatcher, K. 1973. The preference of rats for free or response-produced food. *Anim. Learn. Behav.*, **1,** 241–243.

Houston, A., Kacelnik, A. & McNamara, J. 1982. Some learning rules for acquiring information. In: *Functional Ontogeny* (Ed. D. McFarland), pp. 140–191. London: Pitman.

Hughes, B. O. & Duncan, I. J. H. 1988. The notion of ethological need, models of motivation and animal welfare. *Anim. Behav.*, **36,** 1696–1707.

Hull, C. L. 1943. *Principals of Behavior.* New York: Appleton-Century-Croft.

HyperLogic 1993. *CubiCalc.* California: HyperLogic Corporation.

Inglis, I. R. 1975. Enriched sensory experience in adulthood increases subsequent exploratory behaviour in the rat. *Anim. Behav.*, **23,** 932–940.

Inglis, I. R. 1983. Towards a cognitive theory of exploratory behaviour. In: *Exploration in Animals and Humans* (Eds. J. Archer & L. Burke), pp. 72–116. London: Van Nostrand Reinhold.

Inglis, I. R. 1987. The information-primacy approach: a reply to Kacelnik. *Anim Behav.*, **35,** 926–927.

Inglis, I. R. & Ferguson, N. J. K. 1986. Starlings search for food rather than eat freely available, identical food. *Anim. Behav.*, **34,** 614–617.

Inglis, I. R. & Freeman, N. H. 1976. Reversible effects of ambient housing stimulation upon stimulation-seeking in rats. *Q. Jl exp. Psychol.*, **28,** 409–417.

Inglis, I. R. & Shepherd, D. S. 1994. Rats work for food they then reject: support for the information-primacy approach to learned industriousness. *Ethology*, **98,** 154–164.

Jensen, E. D. 1963. Preference for bar pressing over free-loading as a function of number of unrewarded presses. *J. exp. Psychol.*, **65,** 451–454.

Jensen, G. D., Leung, C. M. & Hess, D. T. 1970. 'Freeloading' in the skinner box contrasted with freeloading in the runway. *Psychol. Rep.*, **27,** 67–73.

Kacelnik, A. 1987. Information primacy or preference for familiar foraging techniques? A critique of Inglis & Ferguson. *Anim. Behav.*, **35,** 925–926.

Kavanau, J. L. 1967. Behavior of captive white-footed mice. *Science*, **155,** 1623–1639.

Kish, G. B. 1966. Studies of sensory reinforcement. In: *Operant Behavior* (Ed. W. K. Honig), pp. 57–83. New York: Appleton-Century-Crofts.

Kleinman, K. M., McLaughlin, R. J., Gerard, I. V., Boxza, D. A. & Clipper, R. C. 1976. Rats' preference for the more effortful of two responses as a function of prior training. *Psychol. Rep.*, **38,** 931–937.

Knutson, J. R. & Carlson, C. W. 1973. Operant responding with free access to the reinforcer: a replication and extension. *Anim. Learn. Behav.*, **2,** 133–136.

Koffer, K. & Coulson, G. 1971. Feline indolence: cats prefer free to response-produced food. *Psychonom. Sci.*, **24,** 41–42.

Konrad, K. & Bagshaw, M. 1970. The effect of novel stimuli on cats reared in a restricted environment. *J. comp. physiol Psychol.*, **70,** 157–164.

Kopp, J., Bourland, G., Tarte, R. D. & Vernon, C. R. 1976. Acquisition of bar pressing in non-deprived rats. *Psychol. Rec.*, **26,** 49–54.

Kosko, B. 1994. *Fuzzy Thinking.* London: Flamingo.

Krebs, J. R. & Kacelnik, A. 1991. Decision making. In: *Behavioural Ecology: An Evolutionary Approach.* 3rd. edn. (Ed. by J. R. Krebs & N. B. Davies), pp. 105–136. Oxford: Blackwell.

Krebs, J. R. & McCleery, R. H. 1984. Optimization in behavioural ecology. In: *Behavioural Ecology, An Evolutionary Approach.* 2nd. edn. (Ed. by J. R. Krebs & N. B. Davies), pp. 91–122. Oxford, Blackwell Scientific Publications.

Krebs, J. R., Kacelnik, A. & Taylor, P. 1978. Test of optimal sampling by foraging great tits. *Nature, Lond.*, **275,** 27–31.

Lamal, P. A. 1978. Reinforcement schedule and children's preference for working versus freeloading. *Psychol. Rep.*, **42,** 143–149.

Larson, L. D. & Tarte, R. D. 1976. The effects of training and effortfulness on rats' choice behaviour in a modified T-maze. *Bull. Psychonom. Soc.*, **7,** 506–508.

Lentz, B. E. & Cohen, S. L. 1980. The effect of prior training on the contrafreeloading phenomenon. *Bull. Psychonom. Soc.*, **15,** 48–50.

Leung, C. M., Jensen, G. D. & Tapley, R. P. 1968. Freeloading in a runway as a function of amount of training and type of reinforcement schedule. *Psychol. Rep.*, **22,** 211–214.

Lima, S. L. 1984. Downy woodpecker foraging behaviour: efficient sampling in simple stochastic environments. *Ecology*, **65,** 166–174.

Mackintosh, N. J. 1974. *The Psychology of Animal Learning.* London: Academic Press.

McLaughlin, R. J., Kleinman, K. M. & Vaugh, L. G. 1973. Effects of prior training at lever pressing on rats' subsequent responding for food or water in the presence of free rewards. *Proc. 81st Ann. Convent. A.P.A.*, **8,** 845–846.

McNamara, J. & Houston, A. 1980. The application of statistical decision theory to animal behaviour. *J. theor. Biol.*, **85,** 673–690.

Melcer, T. & Timberlake, W. 1985. Poison avoidance and patch (location) selection in rats. *Anim. Learn. Behav.*, **13,** 60–68.

Menzel, E. W. 1962. The effects of stimulus size and proximity upon avoidance of complex objects in rhesus monkeys. *J. comp. physiol. Psychol.*, **55,** 1044–1046.

Menzel, E. W. 1991. Chimpanzees (*Pan troglodytes*) problem seeking versus bird-in-hand, least effort strategy. *Primates*, **32,** 497–508.

Mitchell, D. 1976. Experiments on neophobia in wild and laboratory rats: a reevaluation. *J. comp. physiol. Psychol.*, **90,** 190–197.

Mitchell, P. & White, K. G. 1977. Responding in the presence of free food: differential exposure to the reinforcement source. *Bull. Psychonom. Soc.*, **10,** 121–124.

Mitchell, D., Scott, D. W. & Williams, K. D. 1973. Container neophobia and the rat's preference for earned food. *Behavl. Biol.*, **9,** 613–624.

Mitchell, D., Williams, K. D. & Sutter, J. 1974. Container neophobia as a prediction of preference for earned food by rats. *Bull. Psychonom. Soc.*, **4,** 182–184.

Mitchell, D., Becnel, J. R. & Blue, T. 1981. The neophobia-optimality explanation of contrafreeloading in rats: a reassessment. *Behavl Neural Biol.*, **32,** 454–462.

Mitchell, D., Fish, R. C. & Calica, D. R. 1982. Rats respond for food in the presence of free food: how free is the 'free' food? *Learn. Motiv.*, **13,** 257–263.

Montgomery, K. C. 1955. The relation between fear induced by novel stimulation and exploratory behaviour. *J. comp. physiol. Psychol.*, **48,** 254–260.

Morgan, M. J. 1974. Do rats like to work for their food? *Learn. Motiv*, **5,** 352–368.

Morgan, M. J., Einon, D. F. & Nicholas, D. 1975. The effects of isolation rearing on behaviour inhibition in the rat. *Q. Jl exp. Psychol.*, **27,** 625–634.

Nau, K. L., Elias, J. W. & Bell, R. W. 1981. Arousal and bar pressing versus freeloading in Fischer 344 rats. *J. Gen. Psychol.*, **104,** 125–132.

Neuringer, A. J. 1969. Animals respond for food in the presence of free food. *Science*, **16,** 399–40.

Neuringer, A. J. 1970. Many responses for food reward with free food present. *Science*, **169,** 503–504.

Osborne, S. R. 1977. The free food (contrafreeloading) phenomenon: a review and analysis. *Anim. Learn. Behav.*, **5,** 221–235.

Osborne, S. R. & Shelby, M. 1975. Stimulus change as a factor in response maintenance with free food available. *J. exp. Analysis Behav.*, **24,** 17–21.

Pallaud, B. 1971. Contribution a l'étude d'une situation de choix la souris. *Rev. Comporte. Anim.*, **5,** 293–297.

Plowright, C. M. S. & Plowright, R. C. 1987. Oversampling by great tits? A critique of Krebs, Kacelnik, and Taylor's (1978) 'Test of optimal sampling by great tits'. *Can. J. Zool.*, **65,** 1282–1283.

Powell, R. L. 1974. Comparative studies of the preference for free vs response-produced reinforcers. *Anim. Learn. Behav.*, **2,** 185–188.

Rachlin, H. & Baum, W. M. 1972. Effects of alternative reinforcement: does the source matter? *J. exp. Analysis Behav.*, **18,** 231–241.

Rechten, C., Avery, M. & Stevens, A. 1983. Optimal prey selection: why do great tits show partial preferences? *Anim. Behav.*, **31,** 576–584.

Reinhardt, V. 1994. Caged rhesus macaques voluntarily work for ordinary food. *Primates*, **35,** 95–98.

Robertson, L. C. & Anderson, S. C. 1975. The effects of different type and magnitude of reward on the contrafreeloading phenomenon in rats. *Anim. Learn. Behav.*, **3,** 325–328.

Russell, B. 1923. Vagueness. *Austral. J. Phil.*, **1,** 84–92.

Russell, P. A. 1983. Psychological studies of exploration in animals: a reappraisal. In: *Exploration in Animals and Humans* (Ed. J. Archer & L. Birke), pp. 72–116. London: Van Nostrand Rheinhold.

Rutter, S. & Nevin, J. A. 1990. Long-term contrafreeloading in rats during continuous sessions. *Bull. Psychonom. Soc.*, **28,** 556–558.

Sawisch, L. P. & Denny, M. R. 1973. Reversing the reinforcement contingencies of eating and keypecking behaviours. *Anim. Learn. Behav.*, **1,** 189–199.

Shepherdson, D. J., Carlstead, K., Mellen, J. D. & Seidensticker, J. 1993. The influence of food presentation on the behaviour of small cats in confined environments. *Zool. Biol.*, **12,** 203–216.

Shettleworth, S. A., Krebs, J. R., Stephens, D. W. & Gibbon, J. 1988. Tracking a fluctuating environment: a study of sampling. *Anim. Behav.*, **36,** 87–105.

Singh, D. 1970. Preference for bar pressing to obtain reward over freeloading in rats and children. *J. comp. physiol. Psychol.*, **73,** 320–327.

Singh, D. 1972. The pied piper vs the Protestant ethic. *Psychol. Today*, **Jan,** 53–56.

Singh, D. & Query, W. T. 1971. Preference for work over 'freeloading' in children. *Psychonom. Sci.*, **24,** 77–79.

Smith, J. N. M. & Dawkins, R. 1971. The hunting behaviour of individual great tits in relation to spatial

variations in their food density. *Anim. Behav.*, **19**, 695–706.

Smith, J. N. M. & Sweatman, H. P. A. 1974. Food-searching behaviour of titmice in patch environments. *Ecology*, **55**, 1216–1232.

Snygg, D. 1936. Mazes in which the rat takes the longer path to food. *J. Psychol.*, **1**, 153–156.

Stadden, J. E. R. 1983. *Adaptive Behaviour and Learning*. Cambridge: Cambridge University Press.

Stephens, D. W. 1993. Learning and behavioural ecology: incomplete information and environmental predictability. In: *Insect Learning: Ecology and Environmental Perspectives* (Ed. by D. R. Papaj & A. C. Lewis), pp. 195–218. New York: Chapman & Hall.

Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Stephens, R. M., Metze, L. P. & Craig, J. R. 1975. The Protestant ethic effect in a multichoice environment. *Bull. Psychonom. Soc.*, **6**, 137–139.

Stolz, S. B. & Lott, D. F. 1964. Establishment in rats of a persistent response producing a net loss of reinforcement. *J. comp. physiol. Psychol.*, **57**, 147–149.

Studelska, D. R. & Kemble, E. D. 1979. Effects of briefly experienced environmental complexity on open field behaviour in rats. *Behavl Neural Biol.*, **26**, 492–496.

Sunquist, F. & Sunquist, M. 1991. Ocelots and servals. In: *Great Cats* (Ed. by J. Seidensticker & S. Lumpkin), pp 156–161. Emmaus, Pennsylvania: Rodale Press.

Tamm, S. 1987. Tracking varying environments: sampling by hummingbirds. *Anim. Behav.*, **35**, 1725–1734.

Tarte, R. D. 1981. Contra-freeloading in humans. *Psychol. Rep.*, **49**, 859–866.

Tarte, R. D. & Rasmussen, C. T. 1979. Training effects on contra-freeloading in rats housed in operant chambers. *Anim. Learn. Behav.*, **7**, 69–74.

Tarte, R. D. & Snyder, R. L. 1972. Barpressing in the presence of free food as a function of food deprivation. *Psychonom. Sci.*, **26**, 169–170.

Tarte, R. D. & Snyder, R. L. 1973. Some sources of variation in the bar-pressing versus free-loading phenomenon in rats. *J. comp. physiol. Psychol*, **84**, 128–133.

Tarte, R. D. & Vernon, C. R. 1974. Rats barpressing in the presence of free food as a function of fixed-ratio schedules. *Bull. Psychonom. Soc.*, **3**, 34–36.

Tarte, R. D., Townsend, S. G. & Vernon, C. R. 1973. Housing environments and the barpressing vs free-loading phenomenon in rats. *Bull. Psychonom. Soc.*, **2**, 69–71.

Tarte, R. D., Townsend, S. G., Vernon, C. R. & Rovner, L. 1974. An examination of various deprivation-reward combinations in the bar pressing vs freeload-ing phenomenon in rats. *Bull. Psychonom. Soc.*, **3**, 227–229.

Taylor, G. T. 1972. A limitation of the contra-freeloading phenomenon. *Psychonom. Sci.*, **29**, 173–174.

Taylor, G. T. 1975. Discriminability and the contra-freeloading phenomenon. *J. comp. physiol. Psychol.*, **88**, 104–109.

Thistlethwaite, D. L. 1951. A critical review of latent learning and related experiments. *Psychol. Rev.*, **48**, 97–129.

Tolman, E. C. 1932. *Purposive Behavior in Animals and Man*. New York: Appleton-Century-Croft.

Tolman, E. C. 1948. Cognitive maps in rats and men. *Psychol. Rev.*, **55**, 189–208.

Tolman, E. C. 1959. Principles of purposive behaviour. In: *Psychology: A Study of a Science*, Vol 2. (Ed. by S. Koch), pp. 92–157. New York: McGraw-Hill.

Tolman, E. C. & Brunswik, E. 1935. The organism and the causal texture of the environment. *Psychol. Rev.*, **42**, 43–77.

Wallace, R. F., Osborne, S., Norborg, J. & Fantino, E. 1973. Stimulus change contemporaneous with food presentation maintains responding in the presence of free food. *Science*, **182**, 1038–1039.

Wallace, R. J. & Barnett, S. A. 1990. Avoidance of new objects by the black rat *Rattus rattus* after object presentation and change. *Int. J. comp. Psychol.*, **3**, 253–265.

Welker, W. I. 1956. Some determinants of play and exploration in chimpanzees. *J. comp. physiol. Psychol.*, **49**, 84–89.

Welker, W. I. & King, W. A. 1962. Effects of stimulus novelty on gnawing and eating by rats. *J. comp. physiol. Psychol.*, **55**, 838–842.

White, R. W. 1959. Motivation reconsidered: the concept of competence. *Psychol. Rev.*, **66**, 297–333.

Wiltz & Bolton 1971. Exploratory behaviour in response to the spatial rearrangements of familiar stimuli. *Psychonom. Sci.*, **24**, 117–118.

Woods, P. J., Ruckelhaus, S. I. & Bowling, D. M. 1960. Some effects of 'free' and 'restricted' environment rearing conditions upon adult behaviour in the rat. *Psychol. Rep.*, **6**, 191–200.

Woodworth, R. S. 1958. *Dynamics of Behavior*. New York: Holt, Rinehart & Winston.

Zadeh, L. A. 1965. Fuzzy sets. *Inf. Contr.*, **8**, 338–353.

Zadeh, L. A., Fu, K. S., Tanaka, K. & Shimura, M. 1975. *Fuzzy Sets and Their Application to Cognitive and Decision Processes*. New York: Academic Press.

Zimbardo, P. G. & Montgomery, K. C. 1957. Effects of 'free' environment rearing upon exploratory behaviour. *Psychol. Rep.*, **3**, 589–594.