

Operant animal welfare: productive approaches and persistent difficulties

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Abstract

Operant procedures occupy a prominent role within animal welfare science because they provide information about the strength of animals' preferences. It is assumed that strongly motivated choices commonly indicate conditions necessary for uncompromised welfare. A review of the literature shows that members of many species will work for access to resources not commonly provided to them; including a secure resting place (perches for hens or boxes for rodents) and substrates for species-typical activities such as nesting, digging and rooting (in hens, rats, mice and pigs). Despite a recent surge in popularity, operant techniques remain under-utilised and studies employing them struggle to find the best method for prioritising resources. In order to fully exploit the potential of operant procedures a wider appreciation of the relevant theories and techniques might be beneficial; including greater employment of the basic principles of reinforcement theory and further development of more complex economic analogies. If these two strands of research develop together, operant approaches have a key role to play in refining and replacing husbandry practices that undermine animal welfare.

Keywords: animal welfare, economic demand, environmental enrichment, operant conditioning, reinforcement, review

Introduction

Early last century Reinforcement Theory began to take a prominent role within psychology, demonstrating an animal's willingness to work for conditions that it finds enjoyable. This phenomenon was first formalised in Thorndike's 'Law of Effect': "Of several responses made to the same situation, those which are accompanied or closely followed by satisfaction to the animal will, other things being equal, be more firmly connected with the situation, so that, when it recurs, they will be more likely to recur; those which are accompanied or closely followed by discomfort to the animal will, other things being equal, have their connections with that situation weakened, so that, when it recurs, they will be less likely to occur. *The greater the satisfaction or discomfort, the greater the strengthening or weakening of the bond*" (Thorndike 1911, p 244, emphasis added).

Extensive research into 'trial and error learning' followed on from this theory, commonly employing animal subjects and focusing on the potential for satisfying consequences to reward specific behaviours. This line of inquiry developed in conjunction with the philosophy of radical behaviourism, and established operant models of learning as the dominant approach to psychology from the 1920s to the 1960s (Mandler 1996). Towards the end of this period and into the 1970s there was a substantial amount of research that focused, not on the behaviour being trained, but the nature of effective rewards. It was discovered that not only would animals work for food when free food was

available (Osborne 1977) but that stimulation such as light and other seemingly abstract changes could reward behaviour (Barnes & Baron 1961).

Research into these unusual reinforcers was largely eclipsed by an inter-disciplinary shift in philosophy dubbed the Cognitive Revolution (Mandler 1996) — a rejection of radical behaviourists' insistence that intangibles such as thought and emotions should not be used to explain behavioural phenomena. The problem with this behaviourist position (as noted by Kimble 1989) is that for many people it "sacrifices everything of interest and importance to psychology" (p 493). That is, radical behaviourism was ultimately unsatisfying to many modern researchers and their audience, and it was therefore superseded as the most popular philosophy of psychology (Robins *et al* 1999). It must be noted, however, that radical behaviourism's neglect of animal subjectivity (and hence welfare) was replaced by a new cognitive approach in psychology that de-emphasised the study of animals. Psychology began to be routinely defined as 'the study of the human mind and behaviour' and operant animal research declined. Meanwhile, the discipline of ethology became increasingly concerned with experimental animal behaviour, particularly applied ethology which began to focus upon the issue of domestic animal welfare. The use of simple preference tests had already become common as a way of accessing the animal's point of view (Hughes & Black 1973). In 1983 Marian Dawkins proposed an extension of this approach, using an economic analogy to suggest that

resources an animal will work hard to earn are likely to be important for their well-being, a similar importation had previously occurred within psychology (Lea 1978). Underlying this development was an understanding that welfare is largely, primarily or entirely a matter of the animals' feelings (Duncan 1981) and that access to highly motivating resources would be likely to result in the animal experiencing positive feelings (Duncan & Kite 1987).

This amalgam of an economic concept with various ethological procedures was dubbed Economic Demand Theory. Although only limited use was made of specific economic theory this analogy was used to wed animal welfare concerns centred on feelings to operant techniques for assessing reinforcer viability and strength. For ethological researchers this was a vital step that moved from understanding the direction of an animal's preference to determining whether that preference was trivial (Duncan 2006a) or imperative — with the potential to eventually place and prioritise a wide range of interventions intended to improve welfare upon a single scale.

These events have provided animal welfare researchers with two complimentary pools of theory: 1) Reinforcement Theory, which is straightforward but associated with a now unpopular behaviourist philosophy and not at its strongest when dealing with non-food reinforcement and, 2) Economic Demand Theory, which exists in many variations based either upon a rough-hewn economic analogy or, more rarely, direct employment of economic theories such as reservation price to quantify demand (Kirkden *et al* 2003; Kirkden & Pajor 2006). At the present time Economic Demand Theory is the most widely employed and its development has prompted the current, exponential growth in operant research with animal welfare-related goals.

Materials and methods

There has been extensive and vigorous debate about just what the best and most valid economic approach may be, depending on whether the analogy is being correctly applied or based on false assumptions (Dawkins 1983; Houston 1997; Kirkden *et al* 2003). This review attempts to include a broad array of research that captures the essential goal of operant animal welfare research by including the following features: 1) an animal, 2) an operant which is an action the animal may perform to gain access to an environmental resource (eg lever pressing to open a door) and 3) an environmental resource. The majority of studies are open to extensive methodological critique but this is outwith the scope of the current review. Instead we have included experiments in which a functional operant is demonstrated and treated any more specific claims with caution.

The first objective of operant animal welfare research — and primary subject of this review — is to determine whether or not the animal is willing to perform an operant to access a resource. That is, to see whether an animal will learn and perform a specific behavioural response (that would otherwise occur rarely) in order to gain access to this resource. It is presumed that if the animal can perform the operant, but chooses not to, the resource is of little or no value to them (trivial), even if it is preferred under free-choice conditions.

If the operant is weighted with an increasing cost, a figure can be constructed relating the effort required for each access to how often the animal gains access to the resource. This relation may be used to show that the animal will make more of an effort to obtain some resources (versus others). A range of specific measurements are taken to quantify the exact intensity or persistence of the animal's operant responses (Hursh 1980; Kirkden *et al* 2003, for examples). Demand data are most informative when demonstrating a ranking of various resources from most to least reinforcing, or equivalence between resource of known importance and those that are more poorly understood.

Operant approaches have been seen as potentially powerful techniques in animal welfare science. For example: "demand studies... are currently among the most promising indicators of the behavioral and resource requirements of captive animals" (King 2003, p 214). But their use has taken some time to catch on and remains low, even now, when compared with the number of animals and situations where operant approaches would be informative. This delay may be partly due to the specialised training required in economic theory and operant techniques, and the lack of communication between existing expertise in psychology schools and applied research by biologists. Only recently has the total number of studies approached a point where a review is required to appreciate the progress made so far and to identify productive approaches and persistent difficulties.

Review by species

Most operant animal welfare experiments measure effort made by a small group of individually-assessed animals for one resource (or occasionally several different resources). The results are often ambiguous and lend themselves mainly to further development of the procedures employed. However, many experiments also give some indication of the animal's motivation to earn a specific resource, within the constraints of the experimental procedure. Findings are arranged by species with a focus on resources relevant to animal welfare.

Poultry

Hens were the species studied by Marian Dawkins in her landmark study of 1983 and remain one of the most popular species for operant animal welfare experiments. Hens and broilers can be easily shaped to peck a key or push a weighted bar (Clifton 1979; Petherick & Rutter 1990) although in certain situations pecking for food may lead to an increase in feather pecking (Lindberg & Nicol 1994). Hens will work for food when deprived for several hours or placed on a restricted diet (eg Petherick & Rutter 1990; Faure & Lagadic 1994; Bokkers *et al* 2004).

Other basic variables such as light (Prescott & Wathes 2002) may be used to reinforce or bias a key-pecking response. However, fully-feathered hens will not peck for heat when kept at -5°C , opting instead to make behavioural adjustments. Hens with insulating feathers removed will work for heat (Horowitz *et al* 1978) as will chicks (Morrison *et al* 1986, 1987a) especially when deprived of litter or exposed to an air current (Morrison & McMillan 1985; Morrison *et al* 1987b).

Social contact is reinforcing only under appropriate circumstances such as when cocks are offered unfamiliar cocks, or

hens. Hens will not work for cocks and will make only a moderate effort for access to other hens (Duncan & Kite 1987). When social contact is offered without controlling for variables such as dominance it is not always reinforcing. For example, presence of other hens had no consistent effect on willingness to work for a perching area (Olsson & Keeling 2002).

Hens will work for cage features including nest boxes (as much as for food after 20 h of food deprivation [Duncan & Kite 1987]) and perches (working harder than for an enclosure with no perch [Olsson & Keeling 2002]). Only low levels of responding tend to be demonstrated when dust-bathing litter is used as reinforcement (Dawkins 1983; Dawkins & Beardsley 1986; Faure & Lagadic 1994; Gunnarsson *et al* 2000) unless hens are allowed to see the litter while working for it (Matthews *et al* 1993; Widowski & Duncan 2000).

Hens moved through a narrow doorway to access a tunnel for pre-laying pacing (Cooper & Appleby 1997). Hens pecked to enlarge a 1,600 cm² cage that included a motorised 'moving wall' (maintaining it larger than 1,800 cm², 60% of the time [Lagadic & Faure 1987]).

In a study in which hens were able to enter several cages containing different resources, with entry being made more difficult through narrowing of the entrance, less time was spent on grass or near other hens but the same was spent with food, a nest, a perch or woodchips (Bubier 1996). This design elegantly answers the basic question about which preferences are weakly motivated despite not using a procedure where access to the resources was limited by duration or quantity.

Rats and mice

The lever operant developed for rats was easily adapted for mice which showed similar response patterns and willingness to work for food when food deprived (Anliker & Mayer 1956; Roper 1975). Social contact *per se* has not been studied. However, experiments have been developed that allow mice to live in a group cage whilst working on an operant experiment for other resources (Sherwin 2004).

Mice will work for nest material, albeit less than they will work for food. Response rates may (Roper 1975), or may not (Roper 1973) increase with operant price increases. Mice will choose a cage containing nesting material even when it has a (otherwise avoided) grid floor, or when a solid floor with a nest box is offered as the alternative (van de Weerd *et al* 1998). Mice work for the opportunity to burrow in peat (Sherwin *et al* 2004) or sand (Fantino & Cole 1968). Deermice (*Peromyscus* spp) will perform an operant response for the opportunity to dig sand from a tube (King & Weisman 1964).

Mice will press a lever more often for access to a running wheel (Sherwin 1998, 2003) than enclosed extra cage area (eg tunnels; Sherwin 1998). Mice will perform an operant to enter a novel cage (Sherwin 2003) but size of cage has little effect (Sherwin & Nicol 1997) suggesting this reflects motivation to patrol or explore rather than being related to cage size as such.

The operant behaviour of rats in response to food and water deprivation and the effects of a vast array of experimental conditions are very well demonstrated in the literature due to the traditional use of rats as a research animal (Bauman

1991; Sorensen *et al* 2001). Under cold conditions rats will work for gusts of warm air (Matthews 1971). Both male and female rats will perform an operant to get access to mates (Beck 1971; Matthews *et al* 1997; reviewed in Pfaus *et al* 2001). Female rats work harder for contact with familiar female conspecifics than for a range of other conditions including a larger cage and novel objects (Patterson-Kane *et al* 2002). They show the highest levels of responding for a group size of six within a standard, large-sized laboratory cage (Patterson-Kane *et al* 2004).

Rats will perform an operant and learn discrimination tasks for access to a running wheel (Collier & Hirsh 1971; Iversen 1993, 1998) and persist in running on a treadmill tilted to require more effort (Collier & Levitsky 1968). Rats lift heavier weighted doors to access a cage with a nest box rather than an empty cage. They work harder for a nest box than for nesting material, and least of all for an empty cage (Manser *et al* 1998). Rats will bar press for nesting material eg paper (Oley & Slotnick 1970). Rats showed similar low levels of responding for a cage containing fixed wooden blocks, novel objects and their standard home cage (Patterson-Kane *et al* 2002).

Response rates were similar for an empty larger cage and a standard-sized cage (Patterson-Kane *et al* 2002). The way the cage is configured may be an important variable as rats would climb a steeper tunnel to enter a vertically-arranged enriched cage than a horizontal configuration (Nelson *et al* 2003).

Pigs, cattle and sheep

Both reduced ration and delayed delivery of food produce high levels of operant responding in pigs (Lawrence & Illius 1989; Matthew & Ladewig 1994). Animals fed at commercial levels (approximately 60% *ad libitum*) displayed high operant response rates. Adding fibre to the diet in the form of oats hulls and oats reduced response rates for food (Robert *et al* 1997) but adding it in the form of straw did not (Lawrence *et al* 1989). Piglets will learn an operant rewarded with several minutes of heat (Morrison *et al* 1987b). Pigs prefer to have light on and will work for light onset, and for heat (Baldwin & Meese 1977). Moderate levels of responding was shown for brief contact with another pig through a small opening (Matthew & Ladewig 1994). Pigs will work for straw but the intensity of demand is sensitive to factors such as testing in isolation or with a companion, with straw use decreasing when pigs were alone (Pedersen *et al* 2002). They show higher motivation for peat and branches than for straw (Pedersen *et al* 2005). Sows will perform an operant to get access to a larger pen, the level of responding increases prior to farrowing (Haskell *et al* 1997).

Dairy cows readily perform operant responses on a nose plate; they will work hard for food with a nutritional benefit such as concentrated feed (Moore *et al* 1974) and sodium solution when sodium deficient (Bell & Sly 1976, 1979). Calves using an infra-red switch turn on a light for 74% of the day, but earned much lower exposures when light rewards lasted for limited periods (Baldwin & Start 1981). Operant work for social contact has not been studied in adult

cattle, perhaps because they are unlikely to be kept in isolation; however calves will work for social contact, especially if whole body contact is possible (Holm *et al* 2002). Calves will also work for a larger pen area and are observed to buck and gallop when accessing it (Jensen *et al* 2004). Enclosure size and conformation requirements for adult cattle have not been operantly assessed except to show that heifers will work for an opportunity to lie when prevented from doing so for extended periods (Jensen *et al* 2004, 2005).

Sheep will work for salt when salt deficient (Abraham *et al* 1973). They will perform an operant for heat lamps only when shorn (Baldwin 1972). Sheep using an infra-red switch chose to leave the light on 82% of the time, but earned much lower exposures when light rewards were for limited periods (Baldwin & Start 1981).

Foxes and mink

Mink will perform a lever-press or chain-pulling operant for access to food (Hansen *et al* 2002). They show persistent responding to access to water for swimming (Cooper & Mason 2001; Mason *et al* 2001), and for a running wheel (Hansen & Jensen 2005).

Male foxes will work for food and oestrous females and, at a lower level, for contact with other males (Hovland *et al* 2006).

Primates

Various monkeys and apes have been shaped to respond for food (eg Foltin 1991) however primate operant studies tend to focus upon responses to pharmaceuticals rather than environmental variables. Male and female rhesus monkeys (*Macaca mulatta*) will perform an operant for access to a mate (Michel & Keverne 1968; Keverne 1976) and tufted capuchins (*Cebus apella*) choose social contact as persistently as food under similar deprivation conditions (Dettmer & Fragaszy 2000).

Pigeons

Pigeons and doves will perform an operant for food (Brown & Jenkins 1968) and warmth (Budgell 1971; Schmidt & Rautenburg 1975). Male pigeons will key peck for access to females (Gilberston 1975).

Rabbits

When required to circle around a pillar for grass or coarse mix they show similar demand for the two diets (Leslie *et al* 2004). Rabbits show only low levels of responding for increased cage space with the reward duration of three minutes (Jeziarski *et al* 2005).

Fish

Many species of fish have been trained to push a wand for food in order to demonstrate their circadian patterns, taste preferences and ability to select diets with appropriate energy and nutrient qualities (eg Franco *et al* 1991; Sanchez-Vazquez *et al* 1998; Herrero *et al* 2005). Male Siamese fighting fish (*Betta splendens*) will also perform an operant to get access to a female (Sevenster 1973) or to a mirror to which they show an aggressive display (Hogan 1967; Hogan *et al* 1970).

Other species

Many other species have proved amenable to operant training but this research has not extended into animal welfare-related research (eg horse; Myers & Mesker 1960). Operant techniques have even been used successfully with 'lower order' animals such as ants (Cammaerts 2004) and marine molluscs (Cook & Carew 1986).

All animals assessed will perform an operant to demonstrate motivation to satisfy fundamental homeostatic requirements that cannot be met in other ways, such as: food, key nutrients and heat (in the absence of insulating material) as well as essential requirements for perception, such as light. This allows operant techniques to be used to identify deficits and reduce wastage of resources such as food and heating by providing them on demand (Morrison *et al* 1986) as long as the reward duration is adequate (cf Jones & Nicol 1998).

Food is the physical need most commonly studied and the level of work a hungry animal will perform for food reinforcement represents a high point on a potential motivational scale. Typically, non-food resources will not produce response rates or totals as high as for food (Roper 1975; Iversen 1998) however the difference is sometimes negligible suggesting a resource the animal finds very important (Duncan & Kite 1987; Hovland *et al* 2006).

Conspecific social contact has not been widely studied except in relation to sexual behaviour. It is clear that issues such as degree of contact offered, sex, breeding status, familiarity and dominance radically affect the value and function of social contact (Duncan & Kite 1987; Olsson & Keeling 2002; Hovland *et al* 2006) but access to stable social groups or mates is important for many species (Dettmer & Fragaszy 2000; Holm *et al* 2002), and may be more important than many common environmental enrichments for some (Patterson-Kane *et al* 2002). Many studies probably underestimate motivation for social contact by separating the subject and target animals by hard barriers (Matthews & Ladewig 1994; Bubier 1996). For additional discussion see Holm *et al* (2002) and Patterson-Kane *et al* (2001).

In terms of the physical environment, research has focused attention on certain specific resources such as swimming water for mink (Mason *et al* 2001). Where resources are more widely studied, such as dust-bathing material for hens, results may be mixed. There is, however, substantial cross-laboratory support for the provision of nesting boxes (or burrows) and nesting material for mice and rats (King & Weisman 1964; Oley & Slotnick 1970; Roper, 1973, 1975; Manser *et al* 1998; van de Weerd *et al* 1998; Sherwin *et al* 2004), perches for hens (Bubier 1996; Olsson & Keeling 2002) and rooting or farrowing substrates for pigs (Pedersen *et al* 2002, 2005). Most of these strongly-supported resources are not widely provided *in situ*, suggesting a need not only for continued basic research but applied research and outreach activities to encourage implementation.

Conclusions about the most important needs of different animal species are hard to draw given the small number of experiments available and scarcity of species-resource combi-

nations studied at more than one laboratory. However, there seems to be increasing support for the provision of resting or retreat areas and substrates for species-typical activities such as thermoregulation, lying, nesting, rooting or foraging. These data focus our attention on the animals' fundamental need for security and appropriate activity. Further research might be directed, more specifically, at foraging opportunities and appropriate social and human contact.

The connection between recent operant studies and traditional notions of environmental enrichment seems to have limited the scope of the variables under study to what is in the pen rather than what the pen is. It is difficult to find information relating to cage size and configuration that directly compares demand for different husbandry systems currently in use. A few studies demonstrate that animals are motivated to access space outside the home-cage and that they make use of it to display behaviours apparently suppressed in the home cage (eg territory exploration: Sherwin & Nicol 1997; juvenile play: Jensen *et al* 2004; pre-laying or pre-farrowing pacing: Cooper & Appleby 1997; Haskell *et al* 1997). Animals seem less willing to work for temporary expansion of the home cage area.

It would be helpful to see more studies of complete home environments of different sizes and designs in which space is a functional part of the overall design (areas to run, rest, etc; Nelson *et al* 2003). Reward durations may need to be much longer than the seconds or minutes provided in the largely unsuccessful 'moving wall' method (such as by a moving wall; Lagadic & Faure 1987; Jezierski *et al* 2005; by analogy Baldwin & Meese 1977; Baldwin & Start 1981). There are also problems in using door-opening techniques as animals may not be comfortable with intermittent access. For example, sows usually prefer to farrow on a soil surface, but when an operant door-controlled access to the dirt-floored room (away from a concreted-floored room with food and water) the sows' farrowing preference vanished. Even though they continued to earn similar levels of access to the dirt they farrowed equally in the concrete and dirt areas. It seems that the very presence of a door made access seem less safe and certain and undermined the value of the dirt as a farrowing substrate (Hutson & Haskell 1990). An operant such as a narrow or steep passageway might be preferable as an operant because it requires effort from the animal but does not threaten to block access entirely.

Discussion

Two factors may be limiting the impact of operant animal welfare science. Firstly, the experimental designs appear to be somewhat 'hit and miss' with many only partially succeeding in developing a valid method. Secondly, the problems under investigation do not always seem to be clearly conceptualised and understood from the animal's point of view.

Experimental design

There are still many uncertainties or disagreements about how best to measure willingness to work, addressing every possible variable of the experiment and analysis. However,

existence of successful experiments suggests that some 'best guess' solutions are satisfactory and warrant replication. There seems to be a number of persistent difficulties which have contributed to the existence of many recent studies with ambiguous outcomes.

Many studies do not remove the animal from the resource within a fixed period of time (or after an amount of consumption; eg Warburton & Nicol 2001). This avoids disturbing the animal and prevents interruption of natural durations of consumption (Sherwin & Nicol 1995; Cooper & Mason 2000), however it produces an estimate of a reinforcer's strength without restricting its dose (longer duration of reward may either increase or decrease operant responding, see Hutt 1954; Belke 1997). This approach is vulnerable to confounds such as the variable extent to which each resource can be effectively consumed in larger units. For example, a rat's consumption of food rapidly produces satiety reducing willingness to respond for more food, but wheel running may be performed for much longer periods (Iversen 1998). If natural bout lengths are important for the value of a resource, procedures without fixed reinforcement duration can be used to good effect so long as dwelling times and behaviours are fully recorded (Bubier 1996) and demand is not quantified using any measure that relates responses made to reinforcer magnitude (eg by using highest price paid for a single entry instead of elasticity; Cooper & Mason 2001; Hovland *et al* 2006).

Animals in demand experiments tend to show particularly high inter-individual (error) variability (Lawrence & Illius 1989) which, combined with the limited number of subjects typically used, may greatly reduce the sensitivity of this technique. This may lead to ambiguous or false negative findings, particularly when the study does not include a positive control (a resource of known high value such as food). Methods for mitigating this problem include counterbalancing for idiosyncratic responding levels when assigning subjects to experimental conditions, using within-subject designs (Patterson-Kane *et al* 2002), ensuring all subjects are well-trained (as suggested by Hovland *et al* 2006) and/or studying a more uniform sub-group of the species under investigation.

The final issue we wish to discuss in this section is more problematic. Since only a limited number of resources can be assessed using operant techniques (both in a given experiment and in a line of research using the same methodology) there is a pressing need to develop external criteria that can be used to determine when demand is low, moderate or high enough to be considered imperative for good welfare. This review effectively recommends the use of all resources for which operants will be performed. This would be a useful narrowing of the field from all the resources that an animal simply prefers when given free access. More conservatively, we might select the resource (of those studied) for which the highest levels of work are performed. It is difficult to employ any absolute criterion (eg actual number of lever presses) as this is determined largely by the design of the experiment and apparatus.

The use of resources of known high and low value provides the beginnings of an external context against which amounts of work for resources of less well-established value can be interpreted. It is useful to know whether a resource is as highly reinforcing as food for an animal that is food deprived (Roper 1973, 1975; Duncan & Kite 1987) or more reinforcing than an empty cage (Olson & Keeling 2002; Patterson-Kane *et al* 2002; Hansen & Jensen 2005). But often the results are intermediate and there is not, as yet, a clear way to interpret these levels upon some kind of coherent linear scale.

It will also, ultimately, be important to further demonstrate that levels of operant responding relate meaningfully to other indices of overall animal welfare such as health and physiological stress (eg with cortisol levels; Mason *et al* 2001). It is assumed that resources that animals are highly motivated to encounter will tend to improve their overall welfare, however, this assumption remains untested both in general and in establishing what intensity of demand correlates with husbandry imperatives.

The animal's point of view

Some resources that may be important to animals are difficult to present as abstract qualities in the traditional method of conceptualising an independent variable. Doing so tends to strip them of their function and satisfying qualities for the animal. Key examples of resources affected in this way include those that are satisfying only in the presence of social contacts or eliciting stimuli.

For the sake of simplicity, most operant experiments use animals in social isolation. This approach represents a problem when results are affected by isolation stress or interactions between the value of the resource and social contact (as mentioned by Mench & Stricklin 1990 and demonstrated by Pedersen *et al* 2002; Sherwin 2003). Some experiments show that it is possible to have the animals perform an operant (Sherwin *et al* 2004) or consume a resource (Patterson-Kane *et al* 2001) or both (Albentosa & Cooper 2005) within a social context. Social testing should become the norm for animal species that are typically or ideally housed in social groups.

Animals will tend to work harder for a resource if they can see it — and after they have experienced it and make little or no effort when it is out of sight (eg hens demand for cocks and for dust-bathing material; Duncan & Kite 1987; Matthews *et al* 1993; Widowski & Duncan 2000). Externally cued resources are typically deemed less important for welfare as animals presumably do not suffer frustration specific to that resource if they cannot see it (Hughes 1980; Dawkins 1986; Duncan 1998). However, they may arguably suffer frustration just as discomforting related to a general lack of behavioural opportunities that the specific resource would mitigate. They may even suffer a specific frustration but not be biologically prepared to actively seek out a type of resource that, in a natural situation, is exploited on the basis of opportunity (not under their control; see Duncan 2006b) or always freely available.

If locus of motivation is important it is arguably far less important than strength of motivation (see Jensen 1993).

As a more general point, our enjoyment of (and preference for) a resource tends to form and grow with familiarity (Zajonc 1971). So, although the demand levels of an experimental animal that sees and understands a resource might be seen as providing an overestimation of the motivational state of standard, naive commercial animals, studies using animals from these standard conditions may underestimate the potential satisfaction experienced by informed, competent animals under the normal, enriched conditions we are striving to create. This may be another aspect of the ongoing challenge of embracing the implications of positive as well as negative feelings (Koene & Duncan 2001) and diffuse as well as specifically motivated feelings (Wemelsfelder 1997) in animals.

It is important that we provide operants and rewards that can be effortlessly 'understood' by the animal as being safe and functional (Morrison *et al* 1987a, b, c). It would also be useful to have some research into entire systems rather than specific factors — much as Dawkins carried out in her early preference experiments studying free range and battery cage environments for hens (Dawkins 1977). Operant procedures allow us to use a 'top-down' approach where we first identify a high quality environment and then seek to understand the factors that contribute to its success (Koene & Duncan 2001) rather than identifying qualities an animal will work for and then trying to integrate them back together or retrofit them into existing conditions.

Discomforting rewards

A final concern we have, related to appreciating the animal point of view, is that we may sometimes be too quick to assume that an animal which is motivated to earn a reinforcer will, in fact, be satisfied to obtain it and benefit from its consumption. Not only may things we enjoy be bad for our long-term welfare, but behaviour with a reflexive, innate or Pavlovian nature (not included in Thorndike's Law of Effect) may not be under the control of consequences. That is, even if a behaviour causes the animal to experience a consequence it may not be shaped by that consequence, and behaviours that are not operant are not informative about the emotional value of their consequences.

It is clear that, in a general sense, something we enjoy may not be good for us. Animals show demand for sexual behaviour, but uncontrolled breeding can place stressors on domestic animals who do not have access to natural methods for regulating mating opportunities. Fighting is also widely considered a behaviour that may result in stress and injury and should be avoided (Brambell 1965) although the males of some species will work for a chance to posture or attack (eg Hogan *et al* 1970). It seems only reasonable for good husbandry to eliminate situations that are likely to cause long-term harm to the animal (or allow it to harm other animals) — although it might be worth considering the need for alternative sources of excitement to replace those we disallow (such as exploration, foraging or play).

Studies showing that animals may work hard for alcohol or drugs, one class of reinforcer that is not necessarily actively preferred over a non-addicted state once physiological dependence is established. It may be argued that some environmental variables can also get animals 'hooked'. For example, access to a running wheel is reinforcing to several species (eg mink: Hansen & Jensen 2005; rats: Iversen 1998) when provided in a barren environment that the animals wishes to escape, or in conjunction with a highly restricted diet, wheel availability may lead to excessively high levels of running associated with severe weight loss and neurobiology similar to that produced by addiction (Rhodes *et al* 2005).

It is often suggested that a certain observation or physical parameter is the key to understanding an animal's overall welfare such as feelings (Duncan 2005) or longevity (Hurnik 1993), however, any widely agreed definition of animal welfare includes multiple strands such as a preponderance of positive subjective states, a range of appropriate behavioural opportunities and physical health. Operant data should be tied to overall welfare conclusions both through formal collaborative research and informal observation of the animals with highly demanded resources to confirm or establish their function and look for evidence of positive or negative emotional responses.

Conclusions

One of the main reasons for writing this review is to encourage the uptake of operant techniques in a wider range of settings. There is currently an emphasis on some of the most intensively-used animal species on farm and in the laboratory (hens, mice) but an absence of work on others (companion animals, zoo animals) that seems to echo the disproportionate use of these techniques in dedicated research facilities (rather than in applied research or the field).

Discussion of Economic Demand Theory within ethology reinvigorated an important line of inquiry and helped establish the importance of some resources to some animal species. In a few notable cases this research has produced breakthroughs in understanding such as Mason and colleagues' work demonstrating the significant effort made by mink for access to even small amounts of water (Cooper & Mason 2000; Mason *et al* 2001).

The use of Economic Demand Theory may also have some disadvantages for people not inclined to grapple with a relatively complex and flawed body of imported theory. There is a noticeable dearth of experimental publications using economic demand within animal welfare science during the late 80s and early 90s (immediately after Dawkins 1983) and most of the experiments that have emerged since then were carried out by researchers specifically trained in this approach.

The operant animal welfare line of research will continue to depend upon specialised theorists and researchers to untangle the difficult issues of motivation, scaling and validity. However, there is also a need for a wide range of studies to simply establish which existing animal preferences are not trivial and should be prioritised in our

immediate enrichment and refinement efforts, as well as increased use of demand as a component of broader research projects. This might be encouraged by demonstrating the availability of robust, practical and simple alternatives to operant equipment and demand theory.

Most operant animal welfare studies continue to employ some version of the computerised enclosed experimental chamber or operant lever. These methods, derived from psychology, may be replaced in many cases with operants as simple as inclined slopes (Nelson *et al* 2003) or weighted doors (Manser *et al* 1998). Research with an attenuated focus and field location might also employ Reinforcement Theory (not necessarily any more complex than Thorndike's original Law of Effect) rather than Economic Demand Theory to increase uptake, especially in areas where Economic Demand Theory is unfamiliar but Reinforcement Theory is already well established, such as in zoos, with companion animals and in primate laboratories where operant animal training is widely employed for safety, refinement and enrichment purposes.

A broader appreciation of operant procedures might reinvigorate other applications such as the use of operantly controlled learning and foraging devices (especially outside of the zoological situation where such work is already exemplified by Markowitz 1978, 1982) and allowing animals more 'on demand' control of resources may help in reducing wastage (Morrison *et al* 1987a, b, c).

Operant research has the potential to continue to produce breakthroughs in the understanding of animal welfare particularly if it develops in a balanced manner that allows a range of productive approaches to be quickly disseminated in both basic research and application. If this can be accomplished operant approaches exhibit an unparalleled potential to answer immediate husbandry questions, elucidate complex motivational mechanisms, augment and aid in the interpretation of other data, and convey the animal's point of view to a wide audience.

References

- Abraham S, Baker R, Denton DA, Kraintz F, Kraitz L and Purser L** 1973 Components in the regulation of salt balance: salt appetite studied by operant behavior. *Ajebak* 51: 65-81
- Albentosa MJ and Cooper JJ** 2005 Testing resource value in group-housed animals: An investigation of cage height preference in laying hens. *Behavioural Processes* 70: 113-121
- Anliker J and Mayer J** 1956 An Operant Conditioning Technique for Studying Feeding-Fasting Patterns in Normal and Obese Mice. *Journal of Applied Physiology* 8: 667-670
- Baldwin BA** 1972 Operant conditioning techniques for the study of thermoregulatory behavior in sheep. *Journal of Physiology* 226: 41-42
- Baldwin BA and Meese GB** 1977 Sensory reinforcement and illumination preference in the domesticated pig. *Animal Behaviour* 25: 497-507
- Baldwin BA and Start IB** 1981 Sensory Reinforcement and Illumination Preference in Sheep and Calves. *Proceedings of the Royal Society of London. Series B, Biological Sciences*: 513-526
- Barnes GW and Baron A** 1961 Stimulus complexity and sensory reinforcement. *Journal of Comparative and Physiological Psychology* 54: 466-469

- Bauman R** 1991 An experimental analysis of the cost of food in a closed economy. *Journal of the Experimental Analysis of Behavior* 56: 33-50
- Beck J** 1971 Instrumental conditioned reflexes with sexual reinforcement in rats. *Acta Neurobiologia Experientia* 31: 251-262
- Belke TW** 1997 Running and responding reinforced by the opportunity to run: effect of reinforcement duration. *Journal of the Experimental Analysis of Behavior* 67: 337-351
- Bell FR and Sly J** 1976 The assessment of sodium appetite in calves using operant conditioning procedures. *Journal of Physiology* 263: 178-179
- Bell FR and Sly J** 1979 The metabolic effects of sodium depletion in calves on salt appetite assessed by operant methods. *Journal of Physiology* 295: 431-443
- Brambell FWR** 1965 *Report of the Technical Committee to Enquire into the Welfare of Animals Kept Under Intensive Livestock Husbandry Systems*. Her Majesty's Stationery Office: London, UK
- Brown PL and Jenkins HM** 1968 Autosaping of the pigeons key-peck. *Journal of the Experimental Analysis of Behavior* 11: 1-8
- Bokkers EAM, Koene P, Rodenburg B, Zimmerman PH and Spruit BM** 2004 Working for food under conditions of varying motivation in broilers. *Animal Behaviour* 68: 105-113
- Bubier NE** 1996 The behavioural priorities of laying hens: the effect of cost/no cost multi-choice tests on time budgets. *Behavioral Processes* 37: 225-238
- Budgell P** 1971 Behavioural thermoregulation in the barbery dove, *Streptopelia risoria*. *Animal Behaviour* 19: 524-531
- Cammaerts MC** 2004 Operant conditioning in the ant, *Myrmica sabuleti*. *Behavioural Processes* 67: 417-425
- Clifton PG** 1979 Patterson of feeding in the domestic chick II. An Operant Situation. *Animal Behaviour* 27: 821-828
- Cook DG and Carew TJ** 1986 Operant Conditioning of Head Waving in *Aplysia*. *Proceedings of the National Academy of Sciences of the United States of America* 83: 1120-1124
- Collier G and Levitsky DA** 1968 Operant running as a function of deprivation and effort. *Journal of Comparative and Physiological Psychology* 66: 522-523
- Collier G and Hirsch E** 1971 Reinforcing properties of spontaneous activity in the rat. *Journal of Comparative and Physiological Psychology* 7: 155-160
- Cooper JJ and Appleby MC** 1997 Motivational aspects of individual variation in response to nest boxes by laying hens. *Animal Behaviour* 54: 1245-1253
- Cooper JJ and Mason GJ** 2000 Increasing costs of access to resources cause re-scheduling of behavior in American mink, *Mustela vison*: implications for the assessment of behavioural priorities. *Applied Animal Behaviour Science* 66: 135-151
- Cooper JJ and Mason GJ** 2001 The use of operant technology to measure behavioral priorities in captive animals. *Behavior Research Methods: Instruments & Computers* 33: 427-434
- Dawkins M** 1977 Do hens suffer in battery cages? Environmental preferences and welfare. *Animal Behaviour* 25: 1034-1046
- Dawkins MS** 1983 Battery hens name their price: consumer demand theory and the measurement of ethological 'needs'. *Animal Behaviour* 31: 351-364
- Dawkins MS** 1986 Consumer demand theory and the assessment of animal welfare: a reply to Lawrence. *Animal Behaviour* 35: 295
- Dawkins MS and Beardsley T** 1986 Reinforcing properties of access to litter in hens. *Applied Animal Behaviour Science* 15: 351-364
- Dettmer E and Fragaszy D** 2000 Determining the Value of Social Companionship to Captive Tufted Capuchin Monkeys, *Cebus apella*. *Animal Technology and Welfare* 3: 293-304
- Duncan IJH** 1981 Animal rights, animal welfare: a scientist's assessment. *Poultry Science* 60: 489-499
- Duncan IJH and Kite VG** 1987 Some investigations into motivation in the domestic fowl. *Applied Animal Behaviour Science* 18: 387-388
- Duncan IJH** 1998 Behavior and behavioral needs. *Poultry Science* 77: 1766-1772
- Duncan IJH** 2005 Science based assessment of animal welfare: farm animals. *Scientific and Technical Review* 24: 283-492
- Duncan IJH** 2006a Investigating the Feelings of Agricultural Animals. The Humane Care and Use of Agricultural Animals in Research Two Day Conference. *The Scientists Center for Animal Welfare/The Federation of Animal Science Societies*. 22-23 May 2006, St Louis, MO, USA
- Duncan IJH** 2006b The changing concept of animal sentience. *Applied Animal Behaviour Science* 100: 11-19
- Fantino E and Cole M** 1968 Sand-digging in mice: functional autonomy? *Psychonomic Science* 10: 29-30
- Faure JM and Lagadic H** 1994 Elasticity of demand for food and sand in laying hens subjected to variable wind speed. *Applied Animal Behaviour Science* 42: 49-59
- Foltin RW** 1991 An economic analysis of "demand" for food in baboons. *Journal of the Experimental Analysis of Behavior* 56: 445-454
- Franco J, Johnstone ADF and Mackie AM** 1991 Studies of bait preference in the cod, *Gadus morhua* L: characterization of feeding stimulants using an operant conditioning technique. *Fisheries Research* 10: 229-242
- Gilbertson DW** 1975 Courtship as a reinforcement for key pecking in the pigeon *Columbia livia*. *Animal Behaviour* 23: 735-744
- Gunnarsson S, Matthews LR, Foster TM and Temple W** 2000 The demand for straw and feather as litter substrates by laying hens. *Applied Animal Behaviour Science* 65: 321-330
- Hansen SW, Jensen MB, Pedersen LJ, Munksgaard L, Ladewig, J and Matthews L** 2002 The type of operant response affects the slope of the demand curve for food in Mink. *Applied Animal Behaviour Science* 76: 327-338
- Hansen SW and Jensen MB** 2005 Quantitative evaluation of the motivation to access a running wheel or a water bath in farm mink. *Applied Animal Behaviour Science* 98: 127-144
- Haskell MJ, Hutson GD, Dickenson LG and Palmer S** 1997 The pre-farrowing behaviour of sows with operant access to space for locomotion. *Applied Animal Behaviour Science* 51: 51-58
- Herrero MJ, Pascual M, Madrid JA and Sanchez-Vazquez FJ** 2005 Demand-feeding rhythms and feeding-entrainment of locomotor activity rhythms in tench, *Tinca tinca*. *Physiology & Behavior* 84: 595-605
- Hogan JA** 1967 Fighting and reinforcement in Siamese fighting fish, *Betta splendens*. *Journal of Comparative and Physiological Psychology* 64: 356-359
- Hogan JA, Kleist JA, Kleist S and Hutchings CSL** 1970 Display and food as reinforcers in the Siamese fighting fish (*Betta splendens*). *Journal of Comparative and Physiological Psychology* 70: 351-357
- Holm L, Jensen MB and Jeppesen LL** 2002 Calves' motivation for access to two different types of social contact measured by operant conditioning. *Applied Animal Behaviour Science* 79: 175-194
- Horowitz KA, Scott NR, Hillman PE and van Tienhoven A** 1978 Effects of feathers on instrumental thermoregulatory behavior in chickens. *Physiology and Behavior* 21: 233-238
- Houston AI** 1997 Demand curves and welfare. *Animal Behaviour* 53: 983-990
- Hovland AL, Mason G, Boe KE, Steinheim G and Bakken M** 2006 Evaluation of the 'maximum price paid' as an index of motivational strength for farmed silver foxes, *Vulpes vulpes*. *Applied Animal Behaviour Science* 100: 258-279
- Hughes BO and Black AJ** 1973 The preference of domestic hens for different types of battery cage floor. *British Poultry Science* 14: 615-619

- Hughes BO** 1980 The assessment of behavioural needs. In: Moss R (ed) *The Laying Hen and its Environment* pp 149-159. Martinus Nijhoff Publishers: Boston, USA
- Hurnik JF** 1993 Ethics and animal agriculture. *The Journal of Agricultural Ethics* 6(S1): 21-35
- Hursh SR** 1980 Economic concepts for the analysis of behavior. *The Journal of the Experimental Analysis of Behavior* 34: 219-238
- Hutson GD and Haskell MJ** 1990 The Behaviour of farrowing sows with free and operant access to an earth floor. *Applied Animal Behaviour Science* 26: 363-372
- Hutt PJ** 1954 Rate of bar pressing as a function of quality and quantity of food reward. *Journal of Comparative and Physiological Psychology* 47: 235-239
- Iversen IH** 1993 Techniques for establishing schedules with wheel running as reinforcement in rats. *Journal of the Experimental Analysis of Behavior* 60: 219-238
- Iversen IH** 1998 Simple and conditional visual discrimination and wheel running reinforcement in rats. *Journal of the Experimental Analysis of Behavior* 70: 105-121
- Jensen P** 1993 Nest building in domestic sows: the role of external stimuli. *Animal Behavior* 45: 351-358
- Jensen MB, Munksgaard L, Pedersen LJ, Ladewig J and Matthews L** 2004 Prior deprivation and reward duration attest the demand function for rest in dairy heifers. *Applied Animal Behaviour Science* 88: 1-11
- Jensen MB, Tuomisto L and Pedersen LJ** 2004 Locomotor behaviour in dairy calves, the use of demand functions to assess the effect of deprivation. *Applied Animal Behaviour Science* 86: 3-14
- Jensen MB, Pedersen LJ and Munksgaard L** 2005 The effect of reward duration on demand functions for rest in dairy heifers and lying requirements as measured by demand functions. *Applied Animal Behaviour Science* 90: 207-217
- Jeziarski T, Scheffler N, Werner B and Schumacher E** 2005 Demand functions for cage size in rabbits selectively bred for high and low activity in open-field. *Applied Animal Behaviour Science* 93: 323-339
- Jones R and Nicol CJ** 1998 A note on the effect of control of the thermal environment on the well-being of growing pigs. *Applied Animal Behaviour Science* 60: 1-9
- Keverne EB** 1976 Sexual receptivity and attractiveness in the female rhesus monkey. *Advances in the Study of Behavior* 7: 155-200
- Kimble GA** 1989 Psychology from the standpoint of a generalist. *American Psychologist* 44: 491-499
- King JA and Weisman RG** 1964 Sand digging contingent upon bar pressing in deermice, *Peromyscus*. *Animal Behaviour* 12: 446-450
- King LA** 2003 Behavioral evaluation of the psychological welfare and environmental requirements of agricultural research animals' theory, measurement, ethics, and practical implications. *ILAR Journal* 44(3): 211-221
- Kirkden RD, Edwards JSS and Broom DM** 2003 A theoretical comparison of the consumer surplus and the elasticities of demand as measures of motivational strength. *Animal Behaviour* 65: 157-178
- Kirkden RD and Pajor EA** 2006 Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. *Applied Animal Behaviour Science* 100: 29-47
- Koene P and Duncan IJH** 2001 From environmental requirement to environmental enrichment: from animal suffering to animal pleasure. *The Proceedings of the Fifth International Conference on Environmental Enrichment*. 4-9 November 2001, Sydney, Australia
- Lagadic H and Faure J-M** 1987 Preferences of domestic hens for cage size and floor types as measured by operant conditioning. *Applied Animal Behaviour Science* 19: 147-155
- Lawrence AB, Appleby MC, Illius AW and McLeod HA** 1989 Measuring hunger in the pig using operant conditioning: the effect of dietary bulk. *Animal Production* 48: 213-220
- Lawrence AB and Illius AW** 1989 Methodology for measuring hunger and food needs using operant conditioning in the pig. *Applied Animal Behaviour Science* 24: 273-285
- Lea SEG** 1978 The psychology and economics of demand. *Psychological Bulletin* 85: 441-466
- Leslie TK, Dalton L and Phillips CJC** 2004 Preference of domestic rabbits for grass or coarse mix feeds. *Animal Welfare* 13: 57-62
- Lindberg AC and Nicol CJ** 1994 An evaluation of the effect of operant feeders on welfare of hens maintained on litter. *Applied Animal Behaviour Science* 3: 211-227
- Mandler G** 1996 The situation of psychology: landmarks and choice points. *The American Journal of Psychology* 109: 1-35
- Manser CE, Broom DM, Overend P and Morris TH** 1998 Operant studies to determine the strength of preference in laboratory rats for nest-boxes and nesting materials. *Laboratory Animals* 32: 36-41
- Markowitz H** 1978 Engineering environments for behavioral opportunities in the zoo. *The Behavior Analyst* 1: 34-47
- Markowitz H** 1982 *Behavioral Enrichment in the Zoo*. van Nostrand Reinhold: New York, USA
- Mason G, Cooper J and Clarebrough C** 2001 Frustrations of fur-farmed mink. *Nature* 410: 35-36
- Matthews TJ** 1971 Thermal motivation in the rat. *Journal of Comparative and Physiological Psychology* 2: 173-176
- Matthews LR, Temple W, Foster TM and McAdies TM** 1993 Quantifying the environmental requirements of layer hens by behavioural demand functions. In: Nichelmann M, Wieranga HK and Braun HK (eds) *Proceedings of the International Congress on Applied Ethology* pp 206-209, Berlin, Germany
- Matthews LR and Ladewig J** 1994 Environmental requirements of pigs measured by behavioural demand functions. *Animal Behaviour* 47: 713-719
- Matthews TJ, Grigore M, Tang L, Doat M, Kow L-M and Pfaff DW** 1997 Sexual reinforcement in the female rat. *Journal of the Experimental Analysis of Behavior* 68: 399-410
- Mench JA and Stricklin WR** 1990 Consumer demand theory and social behavior: all chickens are not equal. *Behavioral and Brain Sciences* 13: 28
- Myers RD and Mesker DC** 1960 Operant responding in a horse under several schedules of reinforcement. *Journal of the Experimental Analysis of Behavior* 3: 161-164
- Michael RP and Keverne EB** 1968 Pheromones in the communication of sexual status in primates. *Acta Physiologica Scandinavica* 389: 1-80
- Moore CL, Whittlestone WG, Mullord M, Priest PN, Kilgour R and Albright JL** 1974 Behavior responses of dairy cows trained to activate a feeding device. *Journal of Dairy Science* 58: 1531-1535
- Morrison WD and McMillan I** 1985 Operant control of the thermal environment by chicks. *Poultry Science* 64: 1656-1660
- Morrison WD, McMillan I, Bate LA, Otten L and Pei DCT** 1986 Behavioral observations and operant procedure using microwaves as a heat source for young chicks. *Poultry Science* 65: 1516-1521
- Morrison WD, Bate LA, Amyot E and McMillan I** 1987a Performance of large groups of chicks using operant conditioning to control the thermal environment. *Poultry Science* 66: 1758-1761
- Morrison WD, McMillan I and Amyot E** 1987b Operant control of the thermal environment and learning time of young chicks and piglets. *Canadian Journal of Animal Science* 67: 343-347

- Morrison WD, McMillan I and Bate LA** 1987c Effect of air movement on operant heat demand of chicks. *Poultry Science* 66: 854-857
- Nelson K, Patterson-Kane EG and Love J** 2003 Using preference to develop enriched caging for rats. *Animal Technology and Welfare* 2: 85-88
- Oley NN and Slotnick BM** 1970 Nesting material as a reinforcer for operant behavior in the rat. *Psychonomic Science* 21: 41-43
- Olsson IAS and Keeling LJ** 2002 The push-door for measuring motivation in hens: laying hens are motivated to perch at night. *Animal Welfare* 11: 11-19
- Osborne SR** 1977 The free food contra-free-loading phenomenon: A review and analysis. *Animal Learning and Behavior* 5: 221-235
- Patterson-Kane EG, Harper D and Hunt M** 2001 Cage preference of laboratory rats. *Laboratory Animals* 35: 74-79
- Patterson-Kane EG, Hunt M and Harper D** 2002 Rats demand social contact. *Animal Welfare* 11: 327-332
- Patterson-Kane EG, Hunt M and Harper D** 2004 Rats demand for group size. *Journal of Applied Animal Welfare Science* 7: 267-272
- Pedersen LJ, Jensen MB, Hansen SW, Munksgaard L, Ladewig J and Matthews L** 2002 Social isolation affects the motivation to work for food and straw in pigs as measured by operant conditioning techniques. *Applied Animal Behaviour Science* 77: 295-309
- Pedersen LJ, Holm L, Jensen MB and Jorgensen E** 2005 The strength of pigs' preferences for different rooting material measured using concurrent schedules of reinforcement. *Applied Animal Behaviour Science* 94: 31-48
- Petherick JC and Rutter SM** 1990 Quantifying motivation using a computer-controlled push-door. *Applied Animal Behaviour Science* 27: 159-167
- Pfaus JG, Kippin TE and Centeno S** 2001 Conditioning and sexual behavior: a review. *Hormones and Behavior* 40: 291-321
- Prescott NB and Wathes CM** 2002 Preference and motivation of laying hens to eat under different illuminances and the effect of illuminance on eating behaviour. *British Poultry Science* 43: 190-195
- Rhodes JS, Gammie SC and Garland T** 2005 Neurobiology of mice selected for high voluntary wheel-running activity. *Integrative and Comparative Biology* 45: 438-455
- Robins RW, Gosling SD and Craik KH** 1999 An empirical analysis of trends in psychology. *American Psychologist* 54: 117-128
- Robert S, Rushen J and Farmer C** 1997 Both energy and bulk of food effect stereotypic behaviour, Heart rate and feeding motivation of female pigs. *Applied Animal Behaviour Science* 54: 161-171
- Roper TJ** 1973 Nesting material as a reinforcer for female mice. *Animal Behavior* 21: 733-740
- Roper TJ** 1975 Nest material and food as reinforcers for fixed-ratio responding in mice. *Learning and Motivation* 6: 327-343
- Sanchez-Vazquez FJ, Yamamoto T, Akiyama T, Madrid JA and Tabata M** 1998 Selection of macronutrients by goldfish operating self-feeders. *Physiology & Behavior* 65: 211-218
- Schmidt I and Rautenburg W** 1975 Instrumental thermoregulatory behaviour of the pigeon. *Journal of Comparative Physiology* 101: 225-235
- Sevenster P** 1973 Incompatibility of response and reward. In: Hinde RA and Stevenson-Hinde J (eds) *Constraints on Learning: Limitations and Predispositions* pp 265-283. Academic Press: London, UK
- Sherwin CM and Nicol CJ** 1995 Changes in meal patterning by mice measure the cost imposed by natural obstacles. *Applied Animal Behaviour Science* 43: 291-300
- Sherwin CM and Nicol CJ** 1997 Behavioural demand functions of caged laboratory mice for additional space. *Animal Behavior* 53: 67-74
- Sherwin CM** 1998 The use and perceived importance of three resources which provide caged laboratory mice the opportunity for extended locomotion. *Applied Animal Behavior Science* 55: 353-367
- Sherwin CM** 2003 Social context affects the motivation of laboratory mice, *Mus musculus*, to gain access to resources. *Animal Behaviour* 66: 649-655
- Sherwin CM** 2004 The motivation of group-housed laboratory mice, *Mus musculus*, for additional space. *Animal Behaviour* 67: 711-717
- Sherwin CM, Haug E, Terkelsen N and Vadgama M** 2004 Studies on the motivation for burrowing by laboratory mice. *Applied Animal Behavior Science* 88: 343-358
- Sorensen DB, Ladewig J and Lawson LG** 2001 The influence of strain on demand functions for water in rats, *Rattus Norvegicus*. *Scandinavian Journal of Laboratory Animal Science* 1: 1-9
- Thorndike EL** 1911 *Animal Intelligence*. Macmillan: New York, USA
- van de Weerd HA, van Loo PLP, van Zutphen LFM, Koolhaas JM and Baumans V** 1998 Strength of preference for nesting material as environmental enrichment for laboratory mice. *Applied Animal Behaviour Science* 55: 369-382
- Warburton HJ and Nicol CJ** 2001 The relationship between behavioural priorities and animal welfare: a test using the laboratory mouse, *Mus musculus*. *Acta Agricultura Scandinavica* 30: 124-1300
- Wemelsfelder F** 1997 Life in captivity: its lack of opportunities for variable behaviour. *Applied Animal Behavior Science* 54: 67-70
- Widowski TM and Duncan IJH** 2000 Working for a dustbath: are hens increasing pleasure rather than reducing suffering? *Applied Animal Behaviour Science* 68: 39-53
- Zajonc RB** 1971 Brainwash: familiarity breeds comfort. *Psychology Today* 3: 60-64