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The use of demand functions to assess behavioural priorities in farm animals

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Abstract

The use of demand functions to identify the behaviours most important to animals has been advocated widely. The principle is to place increasing cost on the opportunity to perform several behaviours and subsequently to rank these behaviours according to the change in their performance as a function of cost; this change is described by the elasticity of the demand function. However, the method has been criticised for placing the animal in too artificial a setting. Firstly, the animal works repeatedly for short periods of access to a resource, which may interrupt bouts of behaviour; secondly, animals are tested in isolation, which may affect their motivation to perform the target behaviour; and, finally, assumptions regarding the effect of prior deprivation and reward duration on elasticity of demand need to be tested. This criticism, however, is important only if these factors do affect the elasticity of the resulting demand function. This paper reviews experiments that have developed methods to assess the importance of various behaviours to farm animals and that have tested the effect of social context, length of deprivation of a resource and reward duration. It is concluded that the elasticity of demand function may be used to assess the relative importance of various behaviours, but that it is important to make sure that the experimental set-up yields valid estimates of the elasticity of demand.

Keywords: *animal welfare, behavioural priorities, cattle, demand functions, motivation, pig*

Introduction

Focus on the welfare of farm animals has increased interest in ensuring that their behavioural needs are met. Various behaviours may be compromised under production conditions, but some may be more important to the animals than others. It is therefore important to quantify the value of different behaviours and to assess their relative importance for the welfare of farm animals. The use of demand functions has been suggested as a method for assessing behavioural priorities in order to determine which aspects of the housing environment must be improved first (Dawkins 1983, 1990). In addition to being a good method for ranking the importance of different behaviours, this technique can also be used to quantify the relative attractiveness of different resources to stimulate the same behaviour, for instance, by ranking different types of bedding materials or food sources (Ladewig & Matthews 1996).

The use of demand functions to assess behavioural priorities is an approach that has been inspired by economic theory as well as by experimental psychology (Lea 1978; Hursh 1984). In the analysis of human consumer behaviour, it measures to what extent a change in the price of a particular resource affects the demand for that resource, all other things being equal. Applied to animal welfare research, the idea is to place increasing cost on the performance of a behaviour pattern. This is achieved by increasing the amount of work an animal must do to gain access to a resource that enables it to perform the behaviour. Subsequently, the resources are ranked according to the rate of change in performance as a function of cost. This rate of change is also termed the 'elasticity of the demand function' (Lea 1978; Dawkins 1990), and has been used to assess motivational strength in a range of species, for instance, in pigs (Matthews & Ladewig 1994; Ladewig & Matthews 1996), in poultry (Matthews *et al* 1998; Gunnarsson 2002), in mink (Cooper & Mason 1997, 2000; Mason *et al* 2001; Hansen *et al* 2002), in mice (Sherwin 1996; Sherwin & Nicol 1996, 1997, 1998; Warburton & Nicol 2001; Warburton & Mason 2003), and in rats (Sørensen *et al* 2001a; Ladewig *et al* 2002).

When using operant conditioning to quantify behavioural priorities, the animals are housed in controlled conditions and are required to pay a price by performing an operant task (ie to work) to gain access to the resource that allows the animal to perform a certain behaviour (the reward). Only the price per unit of reward is varied while the price of other resources as well as 'income' (available time) is held constant. The price per unit of reward may be varied by varying the number of operant responses required to access a certain amount of the reward (eg Matthews & Ladewig 1994; Sherwin & Nicol 1997), or by varying the weight of push-doors (eg Petherick & Rutter 1990; Mason *et al* 2001;

Olsson & Keeling 2002), or the number of door pushes (Sumpter *et al* 1999), required to gain access to the reward. The change in the number of rewards earned as a function of price per unit of reward is described by the demand function. This is commonly plotted on log: log axes so that the slope of the demand function equals the elasticity of demand (Lea 1978). If the animal works increasingly hard as the price of accessing the resource increases, the demand for the resource is said to be inelastic, and if the rate of responding decreases as the price increases, the demand is said to be elastic (Hursh 1980). By comparing the elasticity of demand for different behaviours, their relative importance may be assessed. The demand function for food is almost inelastic and is often used as a yardstick for rating the value of other resources (Matthews & Ladewig 1994). The elasticity of the demand function provides a readily quantifiable measure for making comparisons between resources, and the simplicity of the concept is intriguing.

However, methodological issues have been raised concerning the use of the traditional operant conditioning techniques to generate demand functions. Firstly, the animal works repeatedly for short periods of access to a resource and thus bouts of behaviour may be interrupted, and, secondly, the motivation to perform a specific behaviour may be exaggerated if this behaviour is the only option (Mason *et al* 1997; Nicol 1997). For instance, the fact that animals of social species are often tested in isolation may influence the results. Finally, important assumptions regarding the effect of the length of deprivation of access to a resource prior to testing, and of reward duration, on the elasticity of demand (Hursh 1984) need to be tested with the relevant species and behaviours in order to establish their validity.

Is it a problem that bouts of behaviour may be interrupted?

A pre-requisite of the use of elasticity of demand functions as a measure of the strength of motivation to access a resource is that the price of performing the target behaviour is varied while all other factors are held constant. Animals tend to compensate for an increase in the price per visit to a resource by increasing the duration of their visits if they are given the opportunity to do so (eg Sherwin & Nicol 1995; Cooper & Mason 2000). Therefore, the duration of access has to be controlled in order to increase the price of one unit of the reward. Controlling reward duration results in animals being asked to repeatedly work for short periods of access to the reward. Presenting short periods of reward repeatedly may interrupt bouts of behaviour and thereby devalue the reward as suggested by Mason *et al* (1997). Social behaviour was emphasised as being especially likely to be sensitive to interruption because the quality of social interaction may be affected.

The effect of interruption of social contact on social behaviour has been examined in domestic calves and piglets (Jensen *et al* 2001). In both species, animals previously housed in pairs were separated for 24 h (by moving one animal to another pen) and then reunited for 24 h in the home pen. In the 'interrupted' situation, the first 42 min after the animals were reunited comprised 12 successive 3.5 min periods, whereas in the 'undisturbed' situation, continuous contact was allowed. In piglets, the interruption of social contact caused the resident animal to direct more flank pushing at the reintroduced pen mate, while the reintroduced pen mate directed more head knocks and bites at the resident piglet. This increase in aggression suggests that if social contact is interrupted in an operant conditioning set-up, aggressive behaviour may be stimulated in piglets. In calves, however, aggressive behaviour was not observed in either of the two situations. Calves sniffed and licked each other more when social contact was interrupted, but no other effects of interruption were found. This increased sniffing and licking may reflect that calves have to re-establish the identity of their pen mate after reunion and it may reflect reinforcement of the social bond between the two animals. The results suggest that in calves, affiliative social motivation is maintained when given short periods of social contact. Together these two parallel experiments show that the effect of interrupting social behaviour may depend on species, and suggest that the effect of interrupting social contact should be assessed before attempting to measure the demand for social behaviour by operant conditioning techniques.

The development of a method to measure social motivation in dairy calves

The results of Jensen *et al* (2001) suggested that affiliative social motivation was maintained in calves when given short periods of social contact, and, subsequently, Holm *et al* (2002) conducted operant tests in which dairy calves worked for access to social contact. In the study by Jensen *et al* (2001), calves were given access to full social interaction; however, in previous studies assessing social motivation in pigs and in mice using operant conditioning techniques, social contact was provided in the form of visual contact or physical nose-to-nose contact (Matthews & Ladewig 1994; Sherwin 1996). Therefore, Holm *et al* (2002) investigated in an operant setting whether the type of social contact provided affected the demand for social contact in calves.

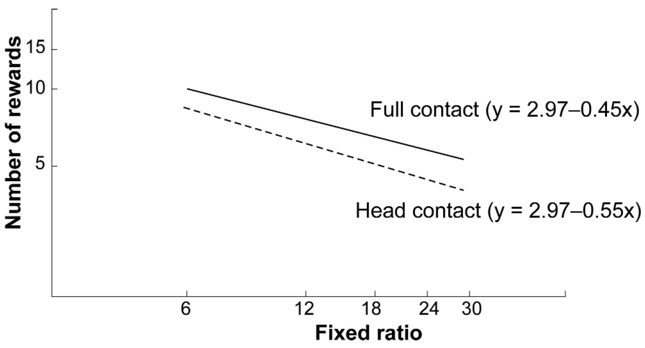
The motivation of calves for two different types of social contact was investigated. The calves had previously been housed in pairs, but during the experiment they were separated and worked (by pressing a panel) for 3 min periods of either full contact or head contact with their pen mate on an ascending Fixed Ratio (FR) schedule. The results showed that the elasticity of the demand function for full social contact was shallower than that for head contact, whereas the intercepts of the two functions did not differ (Figure 1). This suggests full social contact to be more highly valued than head contact alone. The type of social contact given in an operant set-up may thus affect the elasticity of the resulting demand function, and therefore the ranking of social behaviour to other behaviours. In the study on social contact in pigs (Ladewig & Matthews 1996), a surprisingly high elasticity was found for social contact compared to the other resources measured (eg food and straw). This result may have been due to the fact that full social contact was not used as the reward, or alternatively, because interruptions of the contact stimulated aggression in the pigs. In conclusion, calves should be given full social contact in future experiments to obtain a valid estimate of their demand for social behaviour compared to that for other behaviours.

Testing assumptions and the development of a method to measure the demand for rest in dairy cattle

When demand functions are used to rank the importance of different behaviours, the relative elasticity, but not the intensity, of the functions is usually considered. The intensity of a demand function is its elevation relative to the origin. The use of elasticity is based on the assumption that variables such as the level of resource deprivation and reward duration influence the intensity, but not the elasticity of demand (Hursh 1984). That is, if we consider a particular behaviour and if deprivation increases the motivation for this behaviour, then the animal would be expected to take more rewards on all workloads. This will increase the intensity of the demand function while the elasticity remains unchanged. Similarly, animals would be expected to earn more rewards if the reward duration is decreased. There is some support for this (Hursh & Natelson 1981; Matthews *et al* 1998), but testing of the relevant species and behaviours is required.

The effect of the duration of lying deprivation prior to testing on the elasticity and intensity of the demand function has been investigated in dairy heifers (Jensen *et al* in press). Heifers housed in tether stalls were deprived of lying twice daily (morning and afternoon), either for two periods of 3 h or for two periods of 6 h, by attaching a girth strap that was secured to a rafter above the animal. Following the morning deprivation period, the heifers could press a panel for the opportunity to lie down during the subsequent 3 h period. After a given number of panel presses a releasing mechanism in the girth was activated so that the girth hung loose beside the heifer and allowed her to lie down. The FR value varied between 6 and 24 panel presses per reward, and the reward duration was always 15 min. The demand function fitted a straight line when plotted on un-transformed axes, ie a case of non-constant elasticity, and for each of the two demand functions (ie 3 h and 6 h lying deprivation) the elasticity was calculated for each FR value. The length of lying deprivation affected the intensity of the un-transformed demand functions. The heifers earned more rewards the longer the deprivation period. For the shortest deprivation period the elasticity increased over FR values, and at high FR values the demand tended to be more elastic than was the case after the longer deprivation period, suggesting that the demand for lying may be affected by deprivation level (Jensen *et al* in press). Six hours of deprivation and 3 h of testing in which the heifers could work for the opportunity to lie down may have been too mild a deprivation. Tethered heifers have been found to stand for 10 h per 24 h in undisturbed conditions (Jensen 1999), supporting the suspicion that the lowest level of deprivation applied in this experiment was too mild, resulting in a more elastic demand.

Figure 1



Demand functions for two types of social contact (full contact and head contact) in dairy calves. (Reprinted from *Applied Animal Behaviour Science* 79, Holm L, Jensen M B and Jeppesen L L, Calves' motivation for access to two different types of social contact measured by operant conditioning, pp 175–194. Copyright [2002] with permission from Elsevier.)

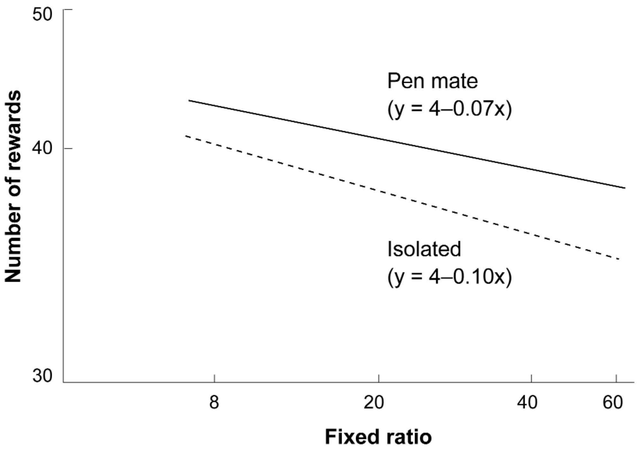
In another experiment, the effect of reward duration on the intensity and the elasticity of the demand function was investigated (MB Jensen *et al* unpublished). Dairy heifers housed in tether stalls were deprived of lying daily for 9 h and could work for the opportunity to lie during the subsequent 6 h period. The price of lying down varied between FR 10 and FR 50, and the reward duration was either 20, 30, 50 or 80 min. The reward duration was found to affect the elasticity of the demand function in that the demand functions for the longer reward durations (30, 50 and 80 min) were shallower than those for the shortest reward duration (20 min). The elasticity of the demand functions for 30, 50 and 80 min did not differ however, suggesting that a reward duration within this range will yield valid estimates of the demand for lying in dairy cattle (MB Jensen *et al* unpublished). In a follow-up experiment, dairy heifers of the same age lay down for 5.5 h during the 6 h period in which they were free to lie down and were tested for 12 h. With a reward duration of 50 mins, these heifers worked to lie down for around 7 h during the 12 h test period in addition to the free 5.5 h of lying (MB Jensen *et al* unpublished), which suggests that heifers have a requirement for lying down of about 12–13 h per 24 h, and that they will work hard to maintain this level.

Is it a problem that animals are tested in isolation?

Another concern that involves the social aspect is that in the traditional setting, operant conditioning tests often involve social isolation. If animals are isolated in a barren operant chamber then social isolation may negatively affect their motivation to interact with the resource. Alternatively, social isolation may enhance their motivation to gain access to the resource because this behaviour is their only option.

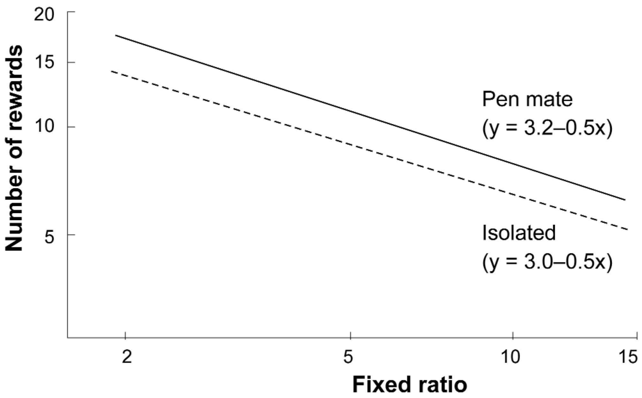
Two experiments, one utilising food and the other, straw, have investigated whether testing in isolation affects the corresponding demand functions in growing pigs (Pedersen *et al* 2002a). In the first experiment, pigs worked for access

Figure 2



Demand functions for food in pigs tested in isolation and with a pen mate positioned in a neighbouring pen. (Reprinted from *Applied Animal Behaviour Science* 77, Pedersen L J, Jensen M B, Hansen S W, Munksgaard L, Ladewig J and Matthews L, Social isolation affects the motivation to work for food and straw in pigs as measured by operant conditioning techniques, pp 295–309. Copyright [2002] with permission from Elsevier.)

Figure 3



Demand functions for straw in pigs tested in isolation and with a pen mate positioned in a neighbouring pen. (Reprinted from *Applied Animal Behaviour Science* 77, Pedersen L J, Jensen M B, Hansen S W, Munksgaard L, Ladewig J and Matthews L, Social isolation affects the motivation to work for food and straw in pigs as measured by operant conditioning techniques, pp 295–309. Copyright [2002] with permission from Elsevier.)

to food either alone or with a pen mate positioned in a neighbouring pen. In the second experiment, pigs worked for access to straw in similar settings. The companion pigs were given a reward whenever the test pigs earned one. The social context in which the pigs were tested was found to affect the demand functions, but the effects differed for the two different resources investigated. The value of food, as indicated by the elasticity of the demand function, was lower when pigs were tested in isolation (Figure 2). The presence of a pen mate did not affect the elasticity of the pigs' demand for straw, but it did increase the intensity of this demand (Figure 3), which means that they earned more straw across all workloads when tested with the pen mate. These experiments illustrate that isolation during testing may affect the demand for a resource and also may affect it in a different way for different resources. In concordance with this, Sherwin (2003) found that mice were more reluctant to work for access to a running wheel when access implied moving away from cage mates, while the presence of cage mates did not affect their tendency to work for access to additional space. Therefore, it may be advisable to avoid isolation during the testing of social species.

The development of a method to measure the relative attractiveness of different rooting materials to pigs

In the traditional experimental set-up, the demand for different resources is measured in a set-up that allows the animals to have access to only one resource at a time (eg Matthews & Ladewig 1994). In such a set-up there may be a risk of over-estimating the demand for less attractive resources since the animals are left with no other alternatives (Mason *et al* 1997). This effect has been shown experimentally in rats, both for different food sources (Lea & Roper 1977) and for different-tasting water solutions (Sørensen *et al* 2001a). When evaluating the relative attractiveness of similar resources, the intensity of the demand function may be considered in addition to its elasticity. A method that includes the intensity in the evaluation of demand functions for closely related resources has been established by Sørensen *et al* (2001b), whereby rats could work for access to two different water solutions simultaneously. Giving animals a simultaneous choice of two closely related resources gives them the opportunity to regulate demand by considering the relative attractiveness of the two resources in addition to the workload imposed (Hursh 1980). Therefore, in order to compare the relative attractiveness of different rooting materials to pigs, the method was developed further using demand functions based on a set-up in which the animals were offered a choice between two different options (Pedersen *et al* 2002b). In the experimental set-up, pigs were given the opportunity to work both for a reference material (long straw) and for one of three alternative materials (peat, branches and chopped straw). Two demand functions were estimated simultaneously: one for the reference material and one for the alternative material. The cross point for the two demand functions was then used as a measure of the relative attractiveness of the alternative material to long straw. The hypothesis was that if two substitutable resources were equally attractive to the animals, the animals would regulate their intake only according to the price of the two resources, which implies that the two demand functions would cross where the prices for the two resources were identical. This hypothesis, which was tested by giving pigs two panels to press at the same time for the same material (ie long straw as the reward on both panels), was confirmed. If the alternative material is preferred over long straw, the pigs would tend to keep on working for the more attractive material even though they could gain access to the less attractive long straw at a lower price. Pedersen *et al* (2002b) showed that if the alternative material was either peat or branches, the pigs continued working for this even though they could gain access to long straw at a lower price. This was not the case for chopped straw. These results thus indicated a higher attractiveness of peat and branches compared to both chopped and long straw.

Elasticity of the demand function and other measures of demand

In recent studies, researchers have tried to overcome potential methodological issues by making the experimental set-up as natural as possible. Animals have been housed in the apparatus, allowed to spend as long as they choose with the resource, and 'near-natural obstacles' have been used instead of the traditional panel or lever pressing operant tasks (see Cooper 2004, pp 47–56, this volume). The advantages of this 'natural' approach are that the researcher does not need to control for the animal's opportunity to perform the behaviour outside the experimental set-up, that bouts of behaviour are not interrupted, and that the animal can access the resources at any time of day. The main disadvantage, however, is that when the time spent with the resource is not controlled, the animal may spend more and more time with the resource as its price increases (eg Collier *et al* 1990; Sherwin & Nicol 1995). This compensatory change invalidates the calculation of elasticity of demand functions because the price per unit of reward is not controlled. For detailed discussions, see commentaries in *Animal Behaviour* (Mason *et al* 1998a,b; Matthews 1998; Sherwin & Nicol 1998).

Other measures of demand, such as the area under the demand function (Houston 1997) or the maximum price paid to gain access to a resource (Hursh *et al* 1988), have also been used to estimate motivational strength. The area under the demand function has been suggested to be a better measure of demand than the elasticity of the demand function (Houston 1997; Kirkden *et al* 2003). However, its use is subject to some controversy (Dawkins 1997). This measure of demand has been used only in a few applied ethological studies (Mason *et al* 2001; Warburton & Mason 2003) and it remains to be validated.

Conclusion and animal welfare implications

Using the elasticity of demand functions to assess behavioural priorities may not be straightforward. When developing this method to assess the motivation for specific behaviours in farm animal species it is important to ensure that the experimental set-up yields valid estimates of the elasticity of demand. For instance, the examples outlined above show that the elasticity of the demand for social contact was lower when calves had access to full social contact; the elasticity of the demand for lying was lower when heifers were given rewards of more than 30 min; and the elasticity of demand for food was lower when pigs were tested with a pen mate. Thus, the degree to which the target behaviour can be performed, the duration of access to perform the target behaviour per reward, and the social context of the test, may all affect elasticity. However, as outlined here, careful experimental testing of the effects of these factors may reveal how valid estimates of the elasticity of demand can be generated. This is a pre-requisite for quantifying the value of different behaviours and for assessing their relative importance for the welfare of farm animals using elasticity of demand functions.

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