COMMENTARIES

A demanding task: using economic techniques to assess animal priorities

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Providing captive animals with the resources they are most motivated to interact with has been proposed as an effective means of improving their welfare (e.g. Dawkins 1983, 1990). Measuring elasticity of demand and income elasticity, two approaches used in microeconomics, was suggested by Dawkins (1983) as a means of ranking resources in terms of their importance to an animal. The elasticity of demand for a particular resource is defined as its change in consumption or usage when made more costly, or more formally, $(dQ/dP) \times (P/Q)$, where Q=quantity and P=price. A demand curve is a plot of this relationship, usually on a log–log plot, with price as the independent variable and amount consumed as the dependent one (e.g. Lea 1978). Resources with inelastic demand are termed necessities, those with highly elastic demand, luxuries. Income elasticity is a related measure, but it involves manipulating a subject's income rather than the price of a resource. It is defined as the proportionate change in the quantity of a commodity that is demanded after a unit proportionate change in a consumer's budget, with prices held constant (e.g. Lea 1978; Bannock et al. 1992). In animal economics, a special case of income elasticity is resilience, the extent to which the performance of an activity decreases when an animal's time budget is reduced (Houston & McFarland 1980; Dawkins 1983; see also Rachlin et al. 1976).

Consumer demand approaches have been much recommended since Dawkins' influential paper, and have recently been put into practice by several authors. Treatments that act as effective perceived costs for hens, *Gallus gallus domesticus*, and mice,

Mus musculus, have been developed (e.g. Faure & Lagadic 1994; Cooper & Appleby 1995; Sherwin & Nicol 1995): hens' motivation to gain access to nestboxes has been shown to be independent of their prior experience of nests (Cooper & Appleby 1995); hens have also been shown to have a high demand for dustbathing substrates (Matthews et al. 1995); and pigs, *Sus scrofa*, in barren conditions have been found to work for the mere sight and sound of a door opening on to an empty compartment (Matthews & Ladewig 1994). These and other recent papers have developed the discussions by Rachlin et al. (1976), Lea (1978), Hursh (1980, 1984), Dawkins (1990) and McFarland (1990) on the factors that affect elasticity and the best ways to generate data with internal and external validity. In several cases, however, they also illustrate what happens when some of these best practices are not followed. In this paper we focus on four guidelines for using consumer demand techniques: (1) that animals be allowed to choose their own bout lengths; (2) that animals be tested in fully closed economies; (3) that cost and resource-use co-vary if the aim is to produce a demand curve; and (4) that animals perceive the imposed costs equivalently for all the resources under consideration. We consider the interpretive problems that ensue if these guidelines are not followed, and suggest means of ensuring they are met when designing experiments.

(1) Letting experimental animals control their own bout lengths has been strongly recommended by several authors (e.g. Houston & McFarland 1980; Sherwin & Nicol 1995), as not doing so may devalue activities for the subject. This is particularly likely for behaviours whose consummation is achieved only after a certain period of performance (e.g. mating), or for activities whose function is reduced by repeated interruption. For example,

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a bird may not embark on a long dustbathing sequence if there is insufficient time to complete it (Hutson 1984), and one can equally imagine that asking an animal to pay for, say, a second of sleep at a time would give quite different results from asking it to pay more for a longer, more useful, bout length. Thus the size of unit offered per unit cost (e.g. the number of wheel-runs, the amount of dustbathing substrate, or the time allowed with a particular item) may affect the elasticity of demand for that activity (e.g. Dawkins 1983).

This effect may account for one finding in a recent study of pig preferences. Matthews & Ladewig (1994) trained pigs to press a panel for access to various resources, and recorded their responses to increasing fixed ratios. Surprisingly, pigs' demand for social contact was only a little less elastic than that for an empty compartment. However, the pigs could work for only 15 s social contact at a time, after which a door would close to separate them, and to gain each successive unit of contact they had to return to the operant panel. Like trying to have a conversation with the phone repeatedly ringing, the interruptions and the short periods of contact may well have devalued the behaviour, revealing little about its importance for pigs in less artificial circumstances.

Offering a fixed unit of reward per access cost is particularly problematic if we want to rank the demands to perform different behaviours. For a start, cutting a bout into short snippets will devalue some activities, but not others (e.g. obtaining food, water, or electrical brain stimulation: reviewed by Matthews & Ladewig 1994). In addition, the actual size of unit offered (e.g. the particular length of time allowed with a resource) is itself likely to affect the rank order of elasticities. To illustrate, Sherwin & Nicol (1996) investigated how mouse behaviour is reorganized in response to increased costs of switching. They found that the time taken for a typical bout differs between behaviours, and that this typical bout length is defended to different extents for different activities. Thus if limits are set by the experimenter over bout lengths, this is likely to affect not only how much an animal values any given behaviour under test, but also how it prioritizes a range of activities. One way of avoiding this problem is to use a suitably designed closed economy set-up, as discussed below.

(2) Testing animals in closed rather than open economies has been widely recommended as giving the most realistic view of animal priorities (e.g. Hursh 1980; Dawkins 1990). In a closed economy, the animal lives with a range of choices and associated costs and benefits over a long timescale; resource-use and costs paid can be quantified by the researcher, and the timescale ensures the animal's behaviour is not a transient artefact (e.g. Hursh 1984; Houston & McNamara 1989). The system of Sherwin & Nicol (1995, 1996) is a good example; mice were individually housed in enclosures for 9 days at a stretch, where they could reach commodities such as running-wheels by traversing a tunnel in which shallow water could be added to impose a price. Such systems contrast with open economy set-ups, for example those in which the animal is put to the test for relatively short periods and spends most of its time housed and fed elsewhere.

As discussed above, one advantage of systems like that of Sherwin & Nicol is that they give animals control over the length and timing of their activity bouts. Closed economies are also recommended because open economies can yield misleading impressions of elastic demand. This is because animals often have a relaxed attitude to resources they learn they can get elsewhere. For example, animals that can obtain food outside the experimental situation tend to show elastic demand for food when tested (e.g. Hursh 1984; Houston & McNamara 1989).

It follows that the type of economy used is crucial when the importance of a number of resources is being compared: it should be the same for all of them, and ideally closed rather than open. Matthews & Ladewig's (1994) study provides an interesting example of where this recommendation was not followed, as their pigs could gain access to one of the resources, social contact, outside the test situation. Although housed singly during the experiment, the pigs were in auditory and olfactory contact with conspecifics, and for 10 min a day they were allowed physical contact too. Thus the set-up was not a fully closed economy with respect to social interaction, and this could well further explain why, under test, social contact seemed worth little more than the sight of an empty compartment. It would be interesting to test pigs who could contact conspecifics only by paying a fee, particularly as the reason the experiment employed this design was that the pigs became disturbed if housed in complete isolation (L. Matthews, personal communication).

(3) Elasticity of demand can be measured only if the price paid and the amount of a resource used co-vary. Thus to increase consumption by 100%, a consumer must double the cost paid, and if the price of a resource doubles, twice the original price must be paid to defend consumption fully (e.g. Lea 1978; Bannock et al. 1992; Matthews & Ladewig 1994). If this is not the case, the data cannot be used to calculate elasticity.

One instance where cost and resource-use do not co-vary is where an animal pays to gain unlimited access to a resource. This is because if an entrance fee doubles, the animal can avoid paying more by visiting the resource half as often as before, and making each of these visits last twice as long. For example, if animals have to perform an operant to reach food, they visit the food less often than when access is free, but compensate by eating more each visit so that the total eaten stays the same (e.g. Collier et al. 1972; Larkin & McFarland 1978). This does not reflect the importance of food, merely that with increasing access price the animal can reschedule its behaviour to use as much of the resource as it ever did. Indeed Sherwin & Nicol's (1996) mouse study demonstrates that this sort of response to increased access costs is true for a wide range of resources, including some one might regard as far less essential than food (e.g. visiting empty compartments and visually inspecting a conspecific), and similar results have also been found for mink, *Mustela vison* (Cooper & Mason 1997a).

Although imposing a price for unlimited access cannot be used to measure elasticity of demand, this has often been overlooked. For example, Sherwin & Nicol (1995), in discussing their finding that an increase in the cost of access did not reduce the total amount eaten by mice, invalidly conclude that this 'support[s] previous studies . . . which show . . . an inelastic demand for food'. Sherwin (1996), in a study using the same set-up but a range of different resources, found results similar to Sherwin & Nicol (1996), namely that the total use of nearly all resources was unaffected by increased access fees, because bout length increased as bout frequency decreased. He concluded that 'none of the resources was perceived as a luxury', an inference that is clearly premature without data suitable for demand curve construction. Cooper & Appleby (1995) also inferred elasticity of demand from inappropriate data. Their hens had to squeeze through a narrow gap to reach an enclosed nestbox. As this gap was made narrower and narrower, so their number of visits declined, but an increase in bout length meant that the total time spent in that part of the cage did not change. As with the mouse studies, these data show that the resource on offer was worth paying for, but because the amount paid and amount of resource used did not co-vary, the authors' conclusion that the hens were showing inelastic demand was not valid.

The relationship between imposed cost and resource-use is important in another way too, as is discussed below.

(4) As emphasized by many researchers (e.g. Matthews & Ladewig 1994; Sherwin & Nicol 1996), it is important that the animal perceives imposed costs equivalently for all the resources under consideration. If there are interactions between the cost imposed and the resources being investigated, a valid ranking of priorities cannot be achieved.

For instance, as Dawkins & Beardsley (1986) and others have pointed out, operants that are difficult for an animal to learn to associate with some commodities would give the misleading impression that these commodities are unimportant. This issue is equally important when imposing other types of barrier or cost: they must not differentially penalize different activities, or the resulting data will be difficult to interpret. Keeling (1994) illustrated this point well. She reduced the amount of space available to hens and recorded the effects on behaviour. In small cages, the birds spent just as much time preening as in large cages, but other behaviour patterns, especially walking, became much less frequent. These data were interpreted as showing something analogous to income elasticity, even though reducing space does not place constraints on a budget, and preening was therefore suggested as more important to hens than walking. However, not only was this manipulation inappropriate for assessing income elasticity, but furthermore, cutting back on space clearly penalizes walking far more than preening. Therefore it simply is not valid to use these data to infer how hens prioritize their activities.

Thus recent studies illustrate some of the many factors that affect elasticity of demand, and that can affect the validity of data. But how can experiments be designed to avoid these pitfalls?

First, as many previous authors have suggested, experiments should use a fully closed economy,

where the animal cannot gain resources (even the sight or smell of them, if this is likely to be important) without paying a price controlled by the experimenter. They should also use costs that do not affect some activities more than others. Matthews & Ladewig (1994) provided a good example of where this was controlled for through the pre-test training of their subjects; their pigs learned the operants with both food and contact with conspecifics as reinforcers. Others recommend using 'natural obstacles', such as narrow gaps, to minimize the risk of operant bias (e.g. Cooper & Appleby 1995).

Meeting the other two guidelines, ensuring that cost and resource-use co-vary while at the same time allowing animals the freedom to schedule their own behaviour, can be more difficult. Matthews & Ladewig (1994), for instance, used a technique that produced exemplary internally valid demand curves, but because it involved prescribing the unit of reward, the data may have limited external validity. One solution is to design the apparatus such that extended bouts of lever-pressing can be used to build up stocks of reward, for example uninterrupted bouts of social contact, a technique that to our knowledge remains unexploited. Another solution is to make interacting with a resource costly in itself, rather than free once an access cost has been paid. For example, Johnson & Cabanac (1982) placed food for rats, *Rattus norvegicus*, in cold chambers, so that the more time they spent eating, the greater the cost they paid in terms of thermoregulation. Faure & Lagadic (1994) used a similar method: hens had to endure exposure to wind while dustbathing, and the effect this had on the length of time they spent bathing in different substrates was recorded. A possible problem with this technique, however, is that it might penalize some activities more than others; for example, cold might particularly penalize swimming, if being wet increases the rate of heat loss, and less so eating, in which the energy gained would help offset the cost paid.

Two further solutions involve abandoning demand curves in favour of other measures. One such measure is income elasticity. This requires altering the subject's budget of time or energy, or even restricting the number of lever-presses a subject can 'spend' per day to reach a range of reinforcers (e.g. Kagel et al. 1980). Such techniques bring with them problems of external validity, however, as the priorities of human con-

sumers, and probably also those of other animals, actually change with budget size (see Mason et al. 1997 for a full discussion of this issue). A second alternative to measuring elasticity of demand is to manipulate access fees and record the maximum the subject will pay to reach a range of resources. For example, primates will tolerate great fixed ratios when lever-pressing for highly addictive psycho-active drugs, but give up responding for less addictive compounds at relatively low fixed ratios (discussed by Dantzer 1990), while hens will perform operants to reach litter that they simply refuse to pay to reach wire flooring (Matthews et al. 1995). This method has two advantages. First, a wider range of costs can be legitimately imposed; demand techniques strictly require that costs impinge on a limited budget, but this method allows the use of aversive stimuli too. Second, it can readily be used in closed economy set-ups where the animal has control over how long it stays with each resource. Using this approach, Cooper & Appleby (1995) showed that the narrowest gap hens will pass through to reach a nestbox depends on their stage in the ovulatory cycle, while Cooper & Mason (1997b) showed that mink will push a heavier door to reach water to swim in than they will to reach a raised look-out platform or an empty compartment.

Overall, generating valid demand curves and rankings of priorities that reflect those of the animal is not just good science: it maximizes the chances of producing results relevant for animal welfare. While the recommendations we discuss here have long been acknowledged, they are still sometimes overlooked in practice. We hope in this paper to have illustrated how the resulting data can give misleading pictures of animal priorities, and also how experiments can be designed that do meet all four guidelines.

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