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Animal economics: assessing the motivation of female laboratory rabbits to reach a platform, social contact and food

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We used novel techniques for assessing resource value to investigate what additions to a barren cage female laboratory rabbits, *Oryctolagus cuniculus*, value. We tested motivation to reach two resources that are potentially practical enrichments: a platform (providing a partly enclosed space and a raised area) and limited social contact with another rabbit through wire mesh and compared these to food and an empty space. To reach these resources, rabbits had to pay entry costs (pushing through weighted doors) which increased every 2 days. With rising costs, rabbits generally rescheduled their behaviour, often reducing visit number and increasing visit length. Measures from economics and behavioural ecology ranked the relative importance of resources similarly (food $\geq$ social contact $\geq$ platform $>$ empty cage). 'Travel cost consumer surplus' (the area under a demand curve of price versus number of visits) ranked food and social contact similarly, but higher than the platform; 'aggregate consumer surplus' (the area under a plot of weight against the number of rabbits paying each price level for the resource) placed food higher than both social contact and the platform; 'reservation price' (maximum weight pushed) did not discriminate between the three resources; and 'expenditure rate' (weight × visits/days) again ranked food and social contact similarly, but higher than the platform. Overall, rabbits' motivation for access to limited social contact thus came close to that for food, suggesting that they value this highly. Rabbits were almost as strongly motivated to be near a platform, but rarely used it, suggesting it might serve a 'bolt hole' function.

Keywords: access costs; animal economics; consumer demand; laboratory rabbit; motivation; *Oryctolagus cuniculus*; resource value

Rabbits, *Oryctolagus cuniculus*, are widely used in research, primarily in medical studies; around 15 000 each year in U.K. (Home Office 2004), and over 260 000 in Europe (European Commission 2005). Changing their housing and husbandry to improve welfare is thus valuable. Recently, concerns have been raised that barren cages not only lead to poor welfare, but also render the laboratory animals poor subjects in some scientific experiments (Würbel 2001; Jain & Baldwin 2003; Sherwin 2004a). How best to improve such cages was our broad aim in this study.

Pair or social housing of female rabbits is recommended where possible (Home Office 1989; Morton et al. 1993). Rabbits are naturally social (Cowan & Bell 1986), with domestic rabbits retaining the social behaviour repertoire of their wild ancestors (Stodart & Myers 1964). Pair or social housing for female laboratory rabbits reduces abnormal behaviour (Whary et al. 1993; Gunn & Morton 1995; Chu et al. 2004), and rabbits may also prefer it to single housing: pair-housed rabbits spend most (88%) of their time close together (Huls et al. 1991). Unfortunately, pair or social housing of female rabbits is not always possible. A recent survey of U.K. pharmaceutical companies

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(Seaman 2002) found that single housing of females was relatively common (46% of rabbits) since it was deemed necessary for certain experiments (Morton et al. 1993; Seaman 2002). Some manufacturers are therefore now providing cages that maintain individual housing, while allowing limited social contact between adjacent rabbits through a grill or clear Perspex. It is not known whether such limited social contact is attractive to rabbits, and assessing this was one goal of the present study.

Enclosed or partly enclosed boxes or shelves may provide another form of enrichment by providing a raised platform and an enclosed 'burrow-like' retreat underneath. Wild rabbits regularly sit on their hindlegs and/or use natural rises for vigilance (Batchelor 1991; Gibb 1993); they also use burrows, bolt holes and vegetation to provide cover from predators (e.g. Kolb 1991). Laboratory rabbits similarly climb on raised areas, apparently for vigilance, exploration or to rest (Whary et al. 1993; Hansen & Berthelsen 2000). Platforms are now provided by some cage manufacturers, and information on rabbits' motivation to have access to platforms is another aspect of the present study.

To determine whether a change to the housing environment leads to improved welfare, a number of approaches are useful. These include observation of the changes in physiology or behaviour, for instance as described above (e.g. Hansen & Berthelsen 2000), and the measurement of an animal's motivation to use the added resources. To do this, costs can be imposed on resource use to assess the extent to which use is defended (Dawkins 1983, 1990; Kilgour et al. 1991; Fraser & Matthews 1997; Mason et al. 2001; Kirkden & Pajor 2006). Costs may be applied prior to resource access, such as increasing ratio schedules for an operant task such as lever pressing (Hursh et al. 1988; Sherwin & Nicol 1997), or overcoming an obstacle such as a narrow gap (Cooper & Appleby 1996) or weighted door (Mason et al. 2001; Olsson & Keeling 2002). Alternatively, costs may be applied continually during resource use (Johnson & Cabanac 1982; Faure & Lagadic 1994). It is important that the tested resources are available to the animal only within the test environment (a 'closed economy'); otherwise animals may refuse to pay the costs while under test, and obtain the resources for free once the test is over (Houston & McNamara 1989; Mason et al. 1998; Ladewig et al. 2002). This type of approach for assessing animals' priorities is now widely used in animal welfare research, but potentially has more general applicability, for instance in studies of foraging, mate choice, parental investment and the circadian scheduling of activities.

Various measures from human economics (e.g. Varian 1993; Begg et al. 2003) can be used to interpret how changes in behaviour with increasing cost relate to the importance of the resource to the animal. Welfare researchers have typically focused on one measure known as the price elasticity of demand (e.g. Dawkins 1983, 1990; Matthews & Ladewig 1994; Gunnarsson et al. 2000). Put simply, if consumption drops with rising cost, demand is said to be 'elastic', while 'inelastic' demand occurs when consumption is defended despite rising cost. However, this measure has several inherent problems (Kirkden & Pajor 2006), including that it can be confounded by satiation (Kirkden et al. 2003; Kirkden & Pajor 2006), that resources that take a greater proportion of the subject's budget tend to be more elastic (e.g. Sloman 1999; Warburton & Mason 2003; Sorensen et al. 2004), and that human economists thus do not use elasticity to assess resource value. Furthermore, to measure price elasticity of demand, there must be a fixed relation between the unit of cost paid and the unit of reward delivered (e.g. Mason et al. 1998), such as a fixed amount of food or water (Hursh et al. 1988) or a fixed period of access to a resource (Gunnarsson et al. 2000). However, if the resource unit is made too small (e.g. access periods are too short), this may devalue certain types of resource (e.g. those that allow sleeping/resting, Jensen et al. 2005; Munksgaard et al. 2005), and it has therefore been argued that animals should be allowed to schedule their own bouts of behaviour (Mason et al. 1998). This was the type of set-up we wanted, but in some variants of this, for example where animals pay a cost on access but can then stay as long as they choose, the price paid and the amount consumed no longer covary (Mason et al. 1998), making it impossible to calculate elasticity meaningfully even if one wanted to.

For all these reasons, we preferred measures other than elasticity of demand. Consumer surplus measures the area under the demand curve of access price versus the amount consumed, and it is used in economics to estimate the value of a resource to human consumers (Ng 1990; Houston 1997; Kirkden et al. 2003). Environmental economists (e.g. Hanley et al. 1997) use a variant called the 'travel cost consumer surplus' to value nonmarket goods such as areas of natural beauty: this is the area under a demand curve of visit price (e.g. journey cost) versus number of visits. 'Aggregate consumer surplus' is the area under an aggregate plot of price versus the number of subjects prepared to pay each price (e.g. Varian 1993). Reservation price is used by economists (e.g. Varian 1993) to refer to the maximum price the consumer is willing to pay for a particular resource (Manser et al. 1996; Mason et al. 2001; Olsson & Keeling 2002; Warburton & Mason 2003; see also Kirkden et al. 2003). This can be thought of as the consumer surplus for the first unit of a resource after a period without (Kirkden et al. 2003). This measure has some advantages: it is one of the few economic measures that, for humans, ranks the value of water above that of diamonds (Begg et al. 2003, page 71), suggesting good validity for welfare work; and it also seems to remain similar whether or not incentive cues from the resources are present (Warburton & Mason 2003), perhaps being most driven by the build-up of internal motivation during deprivation. Finally, we also used expenditure rate (visits × weight/days), i.e. the average expenditure each day on each resource (Warburton & Mason 2003); this measure is loosely derived from optimal foraging theory, and assumes that as expenditure rate increases, the benefit to the animal must also increase (but for critique see Kirkden & Pajor 2006).

Our focus of interest was the motivation of laboratory rabbits to reach limited social contact and a platform. For context, two further resources were provided: food and an empty cage. Use of food as a comparator can be valuable (Dawkins 1983, 1990; Warburton & Mason 2003) since