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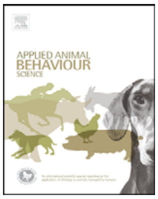

An empirical investigation of two assumptions of motivation testing in captive starlings (*Sturnus vulgaris*): Do animals have an energy budget to 'spend'? and does cost reduce demand?[☆]

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ABSTRACT

The use of demand curves to derive estimates of motivational strength is a popular method for measuring animals' preferences for a range of different resources in applied animal behaviour research. In a typical experiment, an animal pays a gradually increasing cost (e.g. by pushing through a weighted door) in order to access a resource it wants or needs. The resulting demand curves are used to calculate several measures of the strength of the animal's motivation to access the resource. We tested two assumptions that underlie the majority of applications of this approach: first, that animals have a fixed energy budget to spend on access to resources; and second, that the effect of price on demand is not greatly influenced by the order or magnitude of the price changes. Sixteen European starlings (*Sturnus vulgaris*) were trained to push through weighted doors to gain access to one of two resources, either a tray of turf, or protective foliage cover. In the first stage of the experiment reservation prices were established for each bird by daily increasing the force necessary to open the door until the bird no longer accessed the resource. In the next stage, five different forces, chosen to evenly cover the range between free entry and each individual bird's reservation price, were presented in a random order under two levels of food availability. Overall, price was the most important determinant of demand. However, birds' demand for resources was increased by food rationing, suggesting that the cost of pushing the weighted doors might not have been energy. Birds' willingness to pay for a resource was also dependent upon the order in which the forces were presented, and specifically the contrast from the force presented the previous day. The results support the continued use of presenting costs on an ascending order to measure the demand in captive animals, but suggest that random order presentations can be used to check for order effects. We also suggest that the concept of a finite energy budget that animals have to spend on resources may not be useful in the measurement of captive animals' preferences and that a different approach might be needed.

1. Introduction

Measures of motivational strength that involve manipulation of the cost of accessing a resource are a popular method for determining animals' priorities in applied animal behaviour research. In a typical appetence test, the strength of an animal's motivation to obtain a resource

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is measured by systematically manipulating the cost (e.g. the weight of a door or the number of lever presses) that it must pay to obtain the resource, and determining how consumption changes as cost increases (Kirkden and Pajor, 2006). The basic premise underlying this approach is that an animal that is highly motivated to obtain a specific resource will pay a larger cost than a weakly motivated animal. A range of different measures of motivational strength, including elasticity of demand and consumer surplus, can be calculated from demand curves that plot consumption of the resource (i.e. demand) as a function of cost. In applying the results obtained, it is assumed that providing captive animals with resources that they are highly motivated to obtain will improve their welfare. Despite the widespread use of motivation testing in applied ethology, the use of this technique has been under constant criticism since its first inception. Critics have focused on a range of problems including the most appropriate measures of motivational strength (Ng, 1990; Houston, 1997; Kirkden et al., 2003) and a range of methodological issues (Forbes et al., 1997; Bateson, 2004; Kirkden and Pajor, 2006). Here we explore the validity of two assumptions underpinning the use of motivation tests that have not thus far been explicitly tested. First, we test the assumption that animals have a fixed budget to spend on access to resources, and second, we test the assumption that increasing cost decreases demand.

1.1. Assumption 1: animals have a fixed budget to spend

Motivation tests involving the manipulation of costs work under the assumption that there is a common currency with a finite budget, which animals have to spend on the resources presented to them (Lawrence and Illius, 1997; Mason et al., 1997). A finite budget is necessary for the correct application of microeconomics to motivation tests, but the assumption of a limiting budget has rarely been considered empirically. The possibility that energy is a limiting currency, with animals modelled as having an energy budget to spend on resources, is explored in this article.

In microeconomics, decisions are made about how best to spend limited money on resources that will maximize utility or satisfaction (Varian, 2002). Attempts to apply economic theory to the assessment of animal motivation have assumed a direct analogy: the animal is the decision maker and has a limited budget of either energy or time with which to maximize its utility (Dawkins, 1983; Houston and McFarland, 1980). On these grounds, it has been argued that there exist two ways to ascertain which resources are of most importance, one is to increase the cost of a resource and observe the price at which the cost outweighs the motivation to obtain it, and the second is to reduce the income and observe which resources are still paid for.

Reduction of income can be achieved in a number of ways, depending on the limiting currency for behavioural decisions. An example comes from motivation tests with presentation of several resources concurrently. Typically, the price of all resources is increased simultaneously over time (e.g. Mason et al., 2001). In this case, income is reduced because it has to be apportioned between progressively more costly resources. The concept is similar to inflation in human economics where a given salary will not purchase as many goods when inflation makes all goods more expensive (for further explanation see Kirkden and Pajor, 2006). In many experimental paradigms higher costs also take longer to pay (e.g. pressing a lever many times or pushing through doors with heavy weights on), thus increasing costs can also influence the time budget.

An alternative approach has been to manipulate income by reducing day length or duration of resource access (Munksgaard et al., 2005). In these types of experiments, time is limited and this is the currency in which behavioural decisions are made. However, this approach can be criticized because lengthy activities are differentially penalized. For instance, if only a short period of time was available, a tired animal or human might not be expected to sleep, since the utility of sleep is dependent on a lengthy duration.

A typical motivation test is a closed economy, where the animal only has access to resources in the test (Hursh, 1980, 1984; Foster et al., 1997) and uses the free behaviour situation (Lea, 1978), where experimental duration is long and reward duration is unlimited. Since time is not limited, energy is assumed to be the common currency against which behavioural decisions are made (Mason et al., 1997; Lawrence and Illius, 1997). This is a reasonable assumption, since costs used in such tests almost invariably involve a physical challenge, as is the case for lever presses or weighted doors. However, the assumption has never been tested empirically.

The effects of manipulating energy reserves on behaviour have been well studied in the behavioural ecology literature (Caraco, 1981; McNamara and Houston, 1990). Birds only perform non-essential behaviour, such as singing, when they have surplus energy reserves and perform only essential maintenance behaviour when energetically stressed (Houston and McNamara, 1987; Godfrey and Bryant, 2000; Hutchinson et al., 1993; McNamara et al., 1987). Therefore, placing a constraint on the energy reserves available in motivation tests is expected to reduce the amount of luxury behaviour and allow only behaviour that is very important to the animal. In both behavioural ecology experiments and motivation tests, experimenters have manipulated energy reserves by feeding animals more or less food (Godfrey and Bryant, 2000; Bokkers et al., 2004; Olsson et al., 2002). But motivation tests have thus far only manipulated the level of food deprivation in order to manipulate the motivation to obtain a food reward (Bokkers et al., 2004; Olsson et al., 2002). The possibility of reducing income by reducing energy reserves has never been investigated, despite the assumption that energy is the currency used to make behavioural decisions in motivation tests involving physical costs.

We manipulated the energy budget of European starlings by placing them on either a fixed ration diet or on *ad libitum* food and measuring their motivation to obtain two resources, turf or cover. If energy was the limiting factor in this motivation test we would expect birds on rationed diets to have a reduced energetic income

Table 1
Reservation price (g) established using an ascending order and the subsequent five magnet forces used for the random order presentation.

Reservation price	Magnet force 1	Magnet force 2	Magnet force 3	Magnet force 4	Magnet force 5	Number of birds assigned to this series of forces per resource
120	25	50	75	100	125	1 turf
100	20	40	60	80	100	6 cover
80	15	30	45	60	75	2 cover, 7 turf

compared to those on *ad libitum* food and to respond to this by accessing resources fewer times.

1.2. Assumption 2: cost reduces demand

A basic tenet of motivational testing is that by imposing costs upon an item we can reduce demand for that item. Typically, costs are presented in an ascending order, with cost increasing over time (for example see Table 1). However, as cost increases so do a number of other factors including fatigue, boredom, hunger (in food restricted tests), familiarity with equipment and habituation. Hence, increasing cost is confounded by many other factors. It is possible that by not separating these effects from the level of cost, it is these factors and not the cost *per se* that are responsible for observed decreases in demand.

Contrast could also be an important factor in determining demand. In ascending cost orders, animals have to work harder and harder. Sumpter et al. (1999) found that different price manipulations altered measures of demand: animals experiencing a larger increase in force to push open a door, or more lever presses, had more elastic demand curves. This suggests that the magnitude of cost increases in ascending orders can affect measures of motivation.

To separate time and contrast effects from the imposed cost, we presented birds with costs in a random order and analysed the effects of order of presentation, contrast and cost on the demand for turf or cover. An ascending order of costs is typically used because high costs can be built up to gradually, whereas in a random order a high cost might appear early in an experiment and result in extinction of the cost-paying behaviour. Consequently, random orders of cost cannot be used to obtain a complete demand curve (or a measure of maximum price paid) where it is essential to locate the point at which demand falls to zero. The only way to do this is to use an ascending order of costs. Hence, if one wishes to use a random series this must be in addition to an ascending series and this was the method employed in the current experiment. All birds were tested with an ascending order of costs in order to establish the point at which demand fell to zero and then random costs were chosen to fall just below an individual's maximum price paid.

1.3. The experiment

We used the push-door method to impose costs on our birds (see also Olsson and Keeling, 2002; Petherick and Rutter, 1990; Olsson et al., 2002; Widowski and Duncan, 2000). We manipulated the force required to open the push-doors and the cost of access to a resource. Motivation for one of two resources was measured: turf or cover. Therefore, resource type was a between-subjects treatment. These resources were chosen as there is evidence to suggest that starlings might be motivated to obtain them: turf has been found to be a useful form of enrichment for starlings (Asher et al., 2009; Gill et al., 1995) and cover can reduce stress (Witter and Lee, 1995; Lazarus and Symonds, 1992). Because we manipulated the level of food restriction, and turf is a resource associated with the procurement of food in the wild, this might be expected to alter the demand for turf. Food restriction was not expected to alter the demand for cover. Level of food restriction and cost were within-subjects treatments, with all birds being tested at each level of cost twice, once whilst on a fixed ration, and once with food *ad libitum*. We used two methods based on demand curves as measures of motivational strength: consumer surplus and reservation price.

2. Materials and methods

2.1. Subjects

The subjects were 16 wild caught European starlings, 8 males and 8 females, split equally between treatment groups. Prior to the experiment all birds were housed in a large indoor aviary (2.25 m high × 3.60 m wide × 2.40 m deep) furnished with two water baths, floor substrate (wood chippings), and a number of dead branches. Birds were fed a diet of Purina Wild Game Starter at *ad libitum*, supplemented with assorted fruit and mealworms (*Tenebrio* larvae), throughout the experimental period. Birds were held under a 14:10 light:dark cycle under daylight Philips master bulbs of 50 Hz in air conditioned rooms kept between 17 and 20 °C.

2.2. Experimental housing

Individual birds were moved into a closed economy two-chamber preference set-up (each cage measured 0.45 m high × 0.75 m wide × 0.45 m deep, see Fig. 1). They were housed in the experimental housing for the duration of the training and experiment, where they were always able to access the resource cage if they paid the cost of the push-door. The two cages were joined by a transparent Perspex tunnel (0.15 m high × 0.45 m wide × 0.15 m deep), which was bisected by a transparent free-swinging Perspex door. The base of the tunnel was coated with textured Plastikote paint (Valspar, Wheeling, IL, USA) to provide better grip. At the bottom of the free-swinging door was a small strip of metal which came into contact with a solenoid magnet when the door was vertical. Two light beams were positioned on the vertical

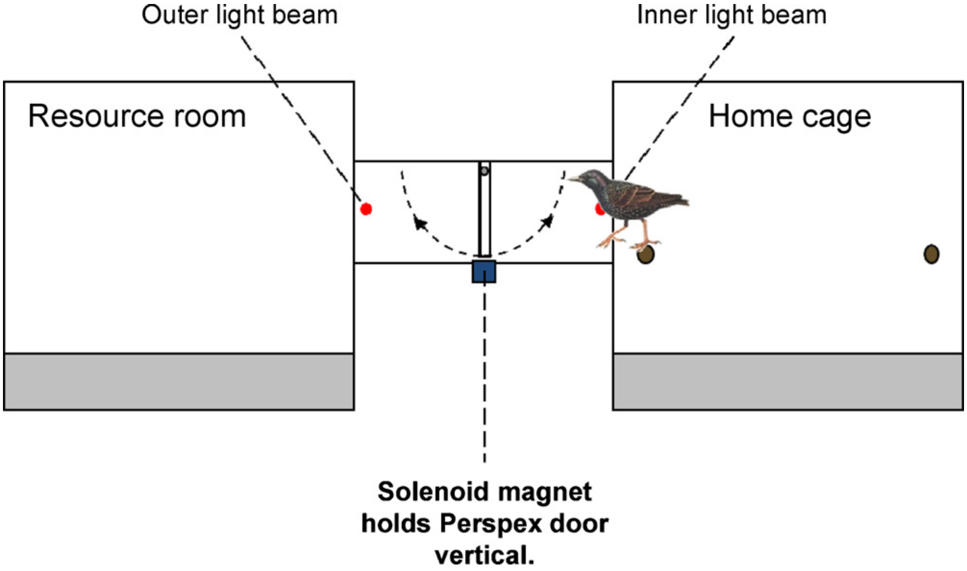

Fig. 1. Equipment used to measure motivational strength (see text for more details).

sides of the tunnel, 5 cm from either end of the tunnel and at a height of 5 cm. The inner beam was located close to the home cage and the outer beam was close to the resource cage. To access the resource cage birds had to push the door off the solenoid, overcoming the magnet's hold on the door and releasing the door to swing freely. The photoreceptors fed into a control box that permitted control of the strength of the solenoid magnet. The control box was linked to a Whisker control system (Cambridge University Technical Services Ltd., Cambridge, UK), which allowed us to monitor when the light beams were broken and switch the solenoid magnet on or off. A programme written in Microsoft Visual Basic 5.0 (Microsoft corporation, Redmond, WA, USA) and using Whisker experimental control language calculated the birds' positions, so that breaking the inner beam followed by the outer beam logged the bird as being in the resource cage and told the Whisker system to switch off the magnet; whereas an outer beam followed by an inner beam break logged the bird as being in the home cage and switched the magnet on. The log of the birds' movements was saved automatically and produced a read-out that included the time of any beam breaks, the position of the bird at all times and whether the magnet was on or off.

There were four identical choice chambers in one room and birds were visually isolated from birds in adjacent cages using translucent white plastic sheeting, to reduce positional biases. Birds did, however, have visual contact with birds in parallel cages. The experiment had four replicates of four birds. Left and right cages were randomly allocated to be the resource cage or the home cage; allocation was constant within birds but was randomized between birds. The resource cage contained either a foraging tray (0.03 m high × 0.45 m wide × 0.44 m deep) filled with turf, or cover. The cover consisted of natural evergreen foliage partially covering three sides of one corner of the outside of the resource cage (see Fig. 2). Cover was maximally protective, providing a hiding place from experimenters, and minimally obstructive, only minimally obstructing the starling's view, since this is the type of cover that has previously been found to reduce starling stress (Witter and Lee, 1995).

2.3. Training

Birds were habituated to the experimental housing with the door held open for two days prior to training, and the resource cage remained empty for the duration of training. We then trained birds to push open the free-swinging door with the magnet switched off. Training sessions began at 1100 and 1600, and lasted 1 h. Birds were food-deprived for 2 h prior to each training session and were given at least 2 h recovery time when food was available *ad libitum*. Shaping was used to train the birds, with each successive approximation to the final response being rewarded with a mealworm (*Tenebrio molitor* larvae). The door was gradually lowered until finally the bird could push through the freely swinging closed door. Training continued until the birds had reached a criterion of entering the resource cage at least five times per day. This took between 1 and 5 days.

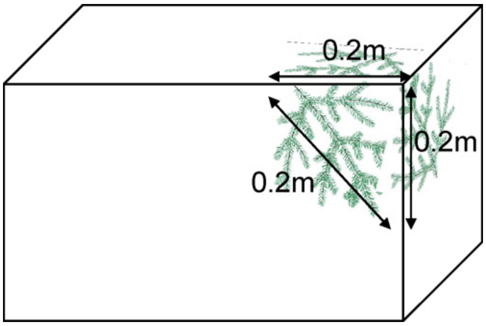

Fig. 2. Cover consisted of an equilateral triangular area (0.2 m^2) of evergreen foliage on three sides of the front corner farthest from the tunnel, with a natural branch also positioned in this corner.

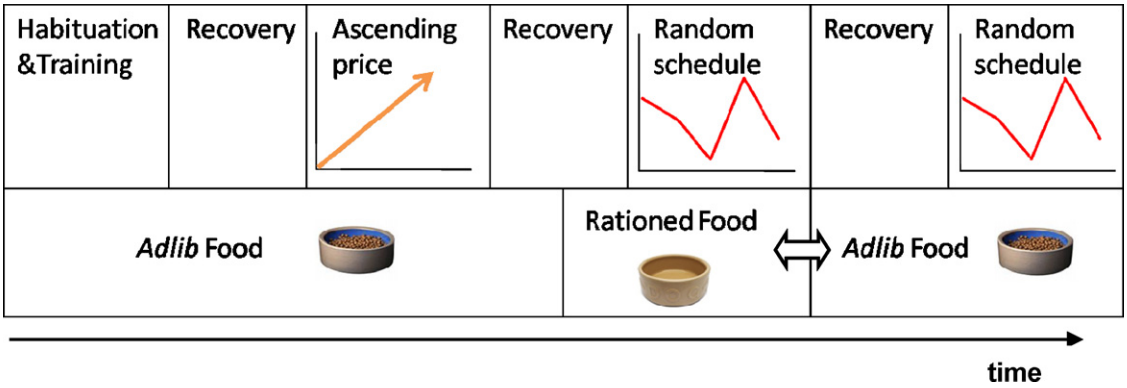

Fig. 3. A timeline of the experimental phases. Birds were placed into the choice chamber set-up and spent 3–7 days in the habituation and training phase. Recovery periods were variable in duration and allowed time for the number of visits to the resource room to stabilize. The ascending price phase followed this and lasted 6–7 days. During these phases birds were on *ad libitum* food. The experimental phase followed. Birds were presented with five costs in a random order (1 per day for 5 days) twice: once when on *ad libitum* food and once on rationed food. The order was counterbalanced between birds, as indicated by the two-way arrow.

After the training criterion had been reached the resource (either turf or cover) was placed in the resource cage and birds' use of the tunnel was monitored over the subsequent 5 days. The experimental procedure only commenced once the number of visits by the birds to the resource cage had stabilized (after approximately 5 days) and therefore the slope of visits against time for 3 days did not differ significantly from 0.

2.4. *Procedure*

The experiment had one between-subjects factor, the resource (turf or cover), and two within-subject factors, the cost to access the resource (magnet strength) and food availability (*ad libitum* or rationed).

First the pushing capacity for individual birds was established to compensate for individual differences in pushing capacity (see Olsson et al., 2002). We did this using the standard paradigm of increasing the force required to open the door and gain access to the resource cage on a daily basis (by 20g per day) until the bird had not entered the resource cage for 2 days. Birds were free to determine the visit duration to the resource cage. Using the highest price paid as an estimate of pushing capacity, we established five equally spaced forces between 0 (free swinging door with magnet switched off) and this maximum. These will henceforth be referred to as scaled magnet strengths. This phase of the experiment was to establish the scaled magnet strengths only and did not form part of the analysis.

The birds had several days of free access (magnet strength 0) to the resource (henceforth referred to as the recovery period) until the number of visits to the resource cage had returned to pre-cost levels. The five equally spaced forces were then presented one per day in a random order until all five forces had been experienced. The order of presentation was randomized between birds but was constant within birds. Birds were then given another recovery period before the forces were presented in the same order, one per day. During one of the presentations of the random order, birds were allowed *ad libitum* access to dry food in the home cage, and during the other presentation and the three days prior to it, the birds' food was rationed. Rationing was constant for each bird but was tailored to the individual based on an amount previously established to hold birds at 90% of their free-feeding weight (between 11 and 15 g). Throughout the experiment all birds were weighed daily by training them to hop on a balance for mealworm rewards. A timeline of the experimental procedure is shown in Fig. 3.

2.5. *Analysis*

In order to validate our manipulation of the energy budget it was necessary to confirm that rationing altered the birds' energy budget. The weights of the birds on the days when recordings took place were analysed using repeated-measures ANOVA with one between-subjects factor, day (1–5), and one within-subjects factor, food availability (two levels: rationed and *ad libitum*).

To quantify the birds' use of the resource cage we calculated a number of measures: frequency of visits to the resource cage; total time spent in the resource cage, visit duration and the number of times the inner light beam was broken per visit. The number of visits to the resource cage was used as the measure of demand for that resource at that particular cost. In pilot investigations the number of visits to an empty cage was almost zero, so we confirmed that birds were paying for the resource and not just the extra space. For number of visits to be a valid measure there would have to be no adjustment in the usage of the resource per visit, which was measured using visit duration. If birds compensated for higher entry costs to the resource room by increasing visit duration, then a single visit to the resource room would not have a constant value to the bird and therefore number of visits would not be a good measure of demand. The number of inner beam breaks per entry was also measured, to establish the number of approaches that were made to the door for each entry. A full factorial linear mixed model was used to discover which factors contributed to demand (number of visits to the resource cage), total time in the resource cage, mean and median visit durations, and beam breaks per entry. Within-subject factors were scaled magnet strength (1–5) and food availability (*ad libitum* or rationed); between-subject factors were the resource (turf or cover) and order of presentation (whether it was the 1st–5th day in that presentation); and force contrast from the previous day (a continuous variable) was a covariate. Force contrast was calculated as the magnet strength for each day minus the magnet strength from the previous day. Non-significant factors were removed to produce the simplest model possible.

We used two economic measures of motivation to assign a value to each resource at each level of food deprivation: reservation price for the first visit and consumer surplus for a satiating amount of turf or cover. Reservation price is the maximum price paid for a single visit to the resource cage, in other words the force above which the bird would no longer enter the resource cage. In order to calculate reservation prices, we found the function that best fitted the inverse demand plots (y = magnet strength against x = visits) for each bird under each condition (*ad libitum* or rationed food). The best fitting function, either a linear ($ax + b$) or quadratic ($ax^2 + bx + c$) equation, was used to calculate the reservation price of a single visit to the resource cage. The best fitting function was also used to calculate the consumer surplus for the satiating amount. We integrated the functions ($\int(ax + b)\,dx = x(2b + ax)/2 : \int(ax^2 + bx + c)\,dx = x(6c + x(3b + 2ax))/6$) and then calculated the area under the curve between $x = 0$ and the value of x when $y = 0$, to give the consumer surplus for the satiating value. This resulted in 32 data points, two per bird (*ad libitum* and rationed), for both the reservation price and the consumer surplus, as well as the R^2 values of the fit between the function and the actual plot. These were analysed using a repeated-measures ANOVA, with one within-subject factor, food availability (*ad libitum* or rationed), and one between-subjects factor, resource (turf or cover).

3. Results

3.1. Food rationing

Birds lost between 2 and 11 g ($\bar{x} \pm$ S.E. $= 6.0 \pm 0.3$ g) of weight when put onto a rationed diet (ANOVA: $F_{1,14} = 18.70$, $P = 0.003$). There was no effect of day (ANOVA: $F_{4,56} = 2.82$, $P = 0.169$) or interaction between day and rationing (ANOVA: $F_{4,56} = 2.61$, $P = 0.187$). Birds' weight had stabilized by the third day of rationing, when the rationed phase of the experiment began, and weight fluctuated by only 1–2 g during this time. When birds were returned to *ad libitum* food they initially consumed more food and their weights were higher than prior to the rationing, but this effect stabilized after 2–4 days and thus did not affect any subsequent treatments. An example of the amount of food consumed and the weight of one typical bird during the experiment is shown in Fig. 4.

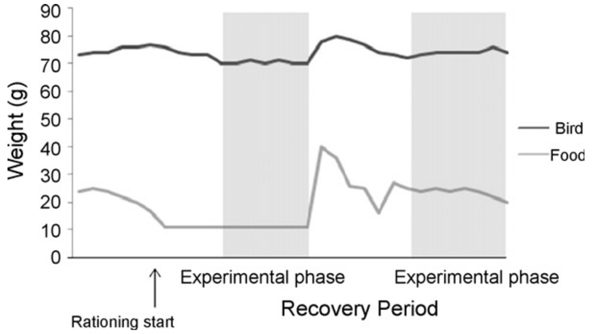

Fig. 4. Example of changes in food consumed and the body weight of a bird throughout the experiment.

3.2. Ascending costs

Birds pushed through doors up to the equivalent of 80–120 g during the initial ascending order treatment ($\bar{x} \pm$ S.E. $= 91.3 \pm 4.1$ g). This set the weights presented in the random order treatment at a minimum of 15, 30, 45, 60 and 75 g and a maximum of 25, 50, 75, 100 and 125 g, depending on individual performance (see Table 1). In the ascending orders, birds receiving turf had a mean reservation price of 85 (±5) g, and birds receiving cover, 95 (±3) g, but there was no significant difference between these scores (T-test: $T_7 = 1.87$, $P = 0.104$).

3.3. Random order of costs: visits to the resource cage

For visit number to be a valid measure of demand, the birds had to show no compensatory increase in visit duration for a reduction in visit frequency (Fig. 5). In fact, shorter visits were found with increased magnet strength (GLMM: $F_{1,4} = 11.78$, $P < 0.001$) and with higher negative contrast from the previous day, although the latter effect diminished in later presentations (GLMM: $F_{1,4} = 6.52$, $P = 0.003$). Furthermore, higher negative contrasts (larger increases in magnet strength from the previous day) were

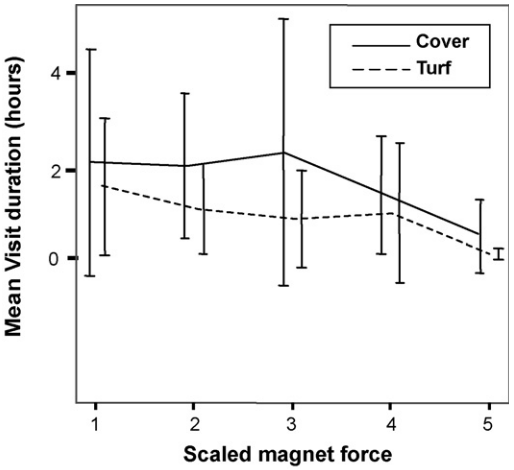

Fig. 5. The duration of visits to each resource when costs (scaled magnet strengths) were presented in a random order (NB: this scale is ordinal and does not represent actual magnitudes of the magnet force). Error bars show ± S.E.

found to increase visit duration at low magnet strength, but to decrease them at higher magnet strengths (GLMM: $F_{1,4} = 23.00$, $P < 0.001$). There was no significant relationship between the duration of visits to the resource cage and visit number (GLMM: $F_{1,1} = 1.82$, $P = 0.196$). The final effect found on visit duration was that the reduction in visit duration with increasing magnet strength was more pronounced in early presentations and when the resource was turf (as shown by the interaction between magnet strength, order and resource, GLMM: $F_{1,19} = 16.02$, $P < 0.001$).

Inner beam breaks were also affected by magnet strength: there were more inner beam breaks at higher magnet strengths and later presentations (interaction between magnet strength and order, GLMM: $F_{1,24} = 3.64$, $P = 0.001$). Contrast in magnet strength from the previous day decreased inner beam breaks per entry when magnet strength was high, but increased it when magnet strength was low (GLMM: $F_{1,4} = 4.29$, $P = 0.009$).

Demand, estimated by the number of visits to the resource cage, decreased as magnet strength increased (GLMM: $F_{1,4} = 4.43$, $P = 0.005$). There was no effect of order on demand in turf, but later presentations resulted in fewer visits when cover was the resource (GLMM: $F_{1,5} = 4.79$, $P = 0.008$). If lower forces came later in the presentation then the number of visits to the resource cage was higher than if they came earlier (GLMM: $F_{1,23} = 6.50$, $P < 0.001$). Finally, all factors were important in determining demand: there was a significant effect of the interaction between resource, food availability, magnet strength and contrast in magnet strength from the previous day (GLMM: $F_{1,15} = 10.21$, $P < 0.001$).

3.4. Random order: economic measures

The functions fitted to the inverse demand plots for each bird under *ad libitum* and rationed food had R^2 values between 0.300 and 0.954 (R^2, $\bar{x} \pm \text{S.E.} = 0.689 \pm 0.026$). There were no within- or between-subjects differences in the R^2 values. The reservation prices for the first visit calculated for the random order condition were higher when birds were on rationed food compared to *ad libitum* food (ANOVA: $F_{1,14} = 11.74$, $P = 0.004$), but there was no effect of resource (ANOVA: $F_{1,14} = 2.53$, $P = 0.134$; see Fig. 6).

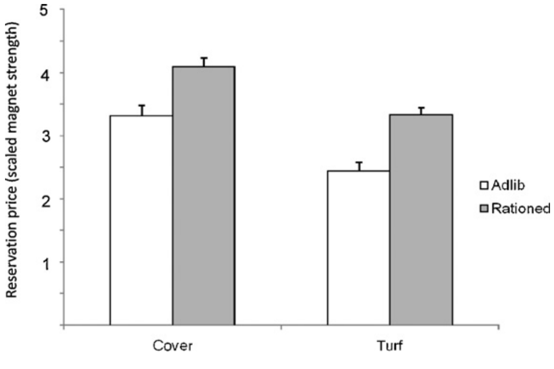

Fig. 6. Mean reservation prices for the first visit ± S.E. when costs (scaled magnet strengths) were presented in a random order.

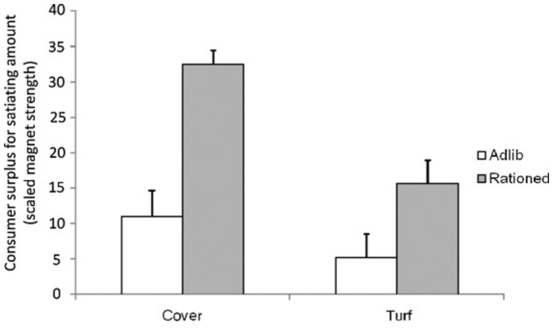

Fig. 7. Mean consumer surplus for the satiating amount ± S.E. when costs (scaled magnet strengths) were presented in a random order.

The consumer surplus for a satiating amount was higher when birds were on rationed food compared to *ad libitum* food (ANOVA: $F_{1,14} = 4.73$, $P = 0.047$), but there was no effect of resource (ANOVA: $F_{1,14} = 0.41$, $P = 0.284$; see Fig. 7).

4. Discussion

We found that by increasing the force required to open a free-swinging door the demand for both turf and cover was reduced, but that other factors including how early a given force appeared in the order of presentation and the contrast with the force experienced the previous day were also important. We also found that hungry birds paid more to obtain cover and turf, indicating that conceptualizing the birds' energy budget as an income to spend on resources may not have been appropriate. Contrary to previous findings in other species (Cooper and Mason, 2000; Marwine and Collier, 1979; Sherwin and Nicol, 1996), starlings did not compensate for reduced visit number by increasing visit duration, and in fact reduced visit duration as the force required to access the resource increased. A tentative suggestion for this finding is that starlings found heavier doors aversive and were therefore more flighty and returned to the home cage faster. Based on the economic measures used here, turf does not appear to be more important than cover to captive starlings, although the measures were not based on complete demand curves and therefore no conclusions should be made from this. Considering starlings pushed open doors that were equivalent to their own body weight, this study would seem to suggest both turf and cover are important to starlings. Since the manner in which turf and cover were presented was always the same, starlings' demand for the general class of turf or cover cannot be inferred. This finding does, however, fit with previous behavioural research on turf (Asher et al., 2009; Gill et al., 1995) and cover (Witter and Lee, 1995; Lazarus and Symonds, 1992) in starlings, although it is a tentative finding because the weight of doors starlings will push for other resources is not known.

4.1. Assumption 1: fixed energy budget

By manipulating the energy available to starlings we altered their motivation for resources other than food. Rationed birds were more motivated to obtain both turf and cover. We established that birds weighed less when on the rationed diet, but it is possible that we did not deplete their energy resources sufficiently to alter the impact of a given cost.

The increased demand for both turf and cover could be explained by an increased motivation to perform foraging behaviour. Hungry birds are expected to spend more time searching for food. In this case we might have expected to see a divergence between the resources, with rationed birds increasing their demand for turf, a resource associated with foraging opportunities, but not for cover. However, this is not what we observed. We have considered three possible explanations for this. First, that increasing visits was an attempt to increase foraging opportunities and starlings were motivated to push open the door when they were hungry to search for food. The resource cages never contained food. However, during training birds were rewarded with mealworms for pushing through the door. Although the time between training and the first treatment was at least seven days, birds may still have regarded pushing open the door as a way to obtain food. Furthermore, energetically stressed animals often display more risk-prone behaviour (Caraco et al., 1980; Barnard and Brown, 1985). If we consider the door as an aversive stimulus and the tunnel and resource cage as a variable food patch, then the increase in door pushes in rationed birds could be explained by a shift to a more risk-prone foraging strategy. A second explanation is that birds responded to food deprivation by increasing overall levels of physical activity. This relates to the above hypothesis because it is one strategy that energetically stressed animals might use to increase the likelihood of finding food (Godfrey and Bryant, 2000). It is supported by Mason et al.'s (2001) finding that mink deprived of access to a food cage increased physical activity. One final explanation is that the mechanisms for increased demand during rationing were different for the different resources. Increased demand for turf might have been related to foraging opportunities, but demand for cover might have been increased due to a reduction in non-maintenance behaviour. For hungry birds without foraging opportunities it might be a better strategy to find a safe resting place to conserve energy, such as was provided by the cover. Unfortunately, no observations or video recordings were made of the resource cages, which may have enabled us to distinguish between these hypotheses.

It may be useful to establish which features of an operant task result in a decrease in demand, to be better able to model animals as consumers and control the currency and budget of motivation tests. Whilst the consumer demand approach, that has been so popular in animal welfare science, requires the assumption of a limiting budget other models do not (Grafen, 2002). The potential of such models in understanding animal motivation needs to be further explored.

4.2. Assumption 2: cost reduces demand

Cost reduced demand in this study. Although demand was also influenced by time (order within a presentation) and cost contrast (increase in force presentation from the previous day), these variables did not have as strong an effect as the cost (strength of the magnet). This provides support for the continued use of ascending order of costs, which are advantageous for reasons outlined in the introduction. However, it is suggested that costs still need to be validated independently of time effects and that a random order of costs could be employed in pilot studies to achieve this.

Evidence from the number of inner beam breaks suggests that cost was responsible for birds not pushing open the door. When cost was higher birds approached the magnet more often. These failed attempts at entry either suggest the animal was unable or unwilling to pay the cost. Alternatively, these visits could have been concerned with environmental monitoring. Starlings are known to value access to areas more if they are visually obscured (Bean et al., 1999). Thus our starlings might have been gaining information through the clear Perspex door that in part compensated for not accessing the resource cage.

Contrast with previously experienced forces also affected the manner in which the birds used the resource cage. A higher contrast (i.e. the door being harder to open than the previous day) reduced visit duration in early presentations. For higher forces, it reduced the number of times the bird approached the tunnel and if birds were presented with the higher forces earlier in the presentation order they made more visits on the lower force presentations. The effects of contrast observed have implications for the level of increment between the costs that should be employed. Bokkers et al. (2004) found differently food-deprived broilers on a fixed ratio of lever presses with an increment of two lever presses per visit had different demand functions for food rewards. However, when using increments of four lever presses the differences were not evident. In addition to the advantages of a greater resolution of measurement, using smaller increments in cost, and therefore reduced contrast from cost experienced the previous day, may be less aversive than larger increments. These advantages must be appraised against the disadvantages of smaller increments, namely the increased experimental duration.

5. Conclusion

We could not establish whether birds had a fixed energy budget to spend on resources because our manipulation of energy also altered the birds' motivation to obtain resources. We suggest the concept of a finite energy budget that animals have to spend on resources may not be useful in the measurement of captive animals' preferences and that a different approach is needed. Costs used to measure animal preferences should be on ascending orders rather than random orders for practical reasons, but random orders should be used to validate the costs used. Since methodological details such as increment in cost and food availability can affect animal preferences, these must be carefully considered in the design and interpretation of such tests.

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