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Accuracy of memory for amount in the foraging starling, *Sturnus vulgaris*

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Abstract. Attempts to include psychological constraints in models of foraging behaviour differ in their assumptions concerning the accuracy of estimation of environmental parameters. Psychologists model estimation error as increasing linearly with the magnitude of a stimulus (Weber's Law), whereas behavioural ecologists either ignore error or assume it to be independent of stimulus magnitude. Studies on the estimation of time intervals have confirmed Weber's Law, but there are few data on the accuracy of estimation of amounts of food. Since the currency of most foraging models is the amount of food acquired per unit of time spent foraging, information on estimation of amount is required. Here, a titration method was used in which starlings chose between two cues. One colour signalled a standard food reward, and the other a reward that adjusted in magnitude according to the birds' choices: it increased when the standard was preferred and decreased when the adjusting option was preferred. There were two standards of 3 and 9 units of food, each of which was delivered at two rates to control for possible effects of rate of reinforcement on discrimination. The observed value of the adjusting option oscillated around a mean value slightly larger than that of the standard. The amplitude and period of these oscillations were larger when the standard was larger, independent of the rate of reinforcement. Also, molecular analysis showed that the probability of choosing the currently larger alternative increased as the relative difference between the adjusting option and standard increased. These results are consistent with Weber's Law applying to starlings' memories for amounts of food.

In traditional optimal foraging models (reviewed in Stephens & Krebs 1986) animals are regarded as perceiving environmental parameters perfectly and remembering them without error. It is acknowledged that introducing estimation error can help to explain quantitative inconsistencies between the predictions of models and experimental data (for examples see Getty & Krebs 1985; Abrahams 1986; Gray & Kennedy 1994). Recent models, however, suggest that introducing estimation error can sometimes lead to the formulation of qualitatively different predictions.

Our first example is Reboreda & Kacelnik's (1991) extension of Scalar Expectancy Theory (SET, for descriptions of this theory see Gibbon et al. 1984; Gibbon 1991) to explain foraging preferences in relation to variability. This is a constrained optimality model in which animals choose the minimum delay to receiving food or the maximum amount of food, subject to constraints imposed by their memories for reward attributes. The crucial assumption is that the memory formed of each percept has a confidence range proportional to its real value, and that memory for the value of a repeatedly experienced stimulus is represented as the distribution of its various perceived values. This generates memory representations that are normally distributed for fixed stimulus sources, and positively skewed for uniformly distributed variable stimulus sources (Gibbon et al. 1988; Reboreda & Kacelnik 1991). For example, memory for the size of rewards from a source that delivers a mixture of two equiprobable amounts would be bimodal and skewed, with its median value to the left of the arithmetic mean of the two amounts. The same would be true for the memory representation of a variable delay. Sampling from such skewed memory representations results in samples that are more frequently smaller than those that would be obtained from the unimodal representation of fixed source with an equivalent mean. Assuming that subjects choose by sampling their memories and prefer bigger reward sizes and shorter delays, the model predicts that when faced with foraging options with equivalent means animals will prefer a more

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variable option when variability is in delay but will prefer a less variable option when variability is in amount (see Reboreda & Kacelnik 1991; Bateson & Kacelnik, in press, for demonstrations of this prediction in starlings). Thus, it is possible that experimental results concerning response to variability, functionally interpreted in the context of risk-sensitive foraging theory (Caraco et al. 1980; Stephens 1981), may at a mechanistic level be the outcome of rate maximizing with estimation error.

Yoccoz et al. (1993) also produced unexpected predictions for sequential-encounter prey choice by introducing error in the estimation of amount and time into an unconstrained optimality model. They assumed explicit relationships between the real energy content and handling time of each food item and what the forager estimates these quantities to be. Yoccoz et al. represented the actual gains and times as random variables G and T, and the animal's perception of these as random variables, X and Y, respectively. They constructed X and Y from G and T by adding normally distributed errors with a mean of zero such that $X=G+E_G$ and $Y=T+E_T$. Their central assumption in the present context is that the variances of the errors E_G and E_T are independent of the actual gains and times, G and T.

Thus, a major difference between Yoccoz et al.'s model and that of Reboreda & Kacelnik lies in the estimation error: the former assumes that estimation error is independent of the magnitude of the quantities being estimated, whereas the latter assumes that it is proportional to the magnitude of the quantity being remembered. To progress with modelling the effects of perceptual error on decision making we need to understand its nature.

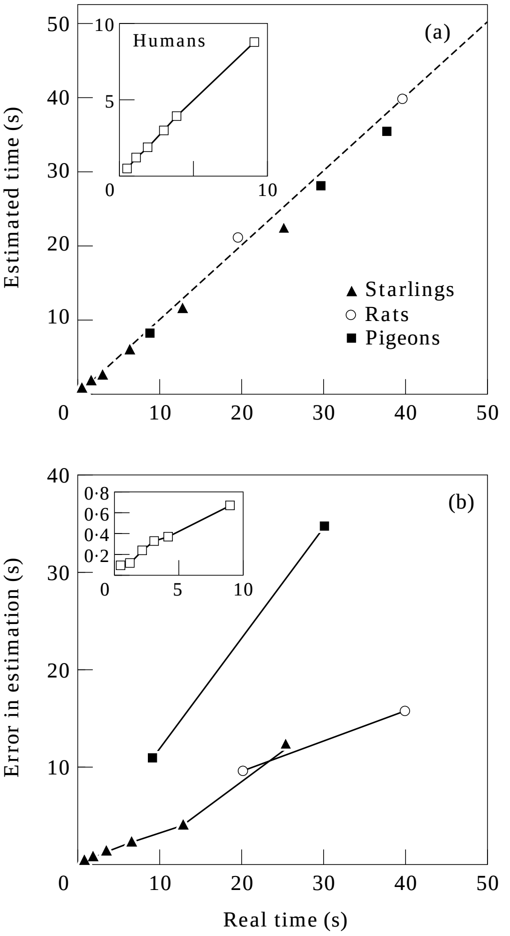

Figure 1. Examples of (a) estimated time and (b) error in estimation of time, both versus actual time, from experiments in which subjects were required to reproduce time intervals. Data are replotted from the following sources: humans from Treisman (1963), starlings from Brunner et al. (1992), rats, *Rattus norvegicus*, from Roberts (1981) and pigeons from Cheng & Roberts (1991). The details of the experiments and the measures of central tendency and error used vary between studies.

Subjective Estimation and Weber's Law

For well over a century psychologists have investigated the relationship between the physical and subjective magnitudes of stimuli (Marks 1974; Dember & Warm 1979). In early experiments human subjects were asked to estimate which of two weights was heavier, or which of two lights brighter, to discover the smallest physical difference necessary for a subjective difference to be reported: the just noticeable difference, or JND. Such experiments led to the formulation of Weber's Law: $\Delta I/I=k$, where I is the physical magnitude of a standard stimulus, ΔI is the change in I necessary for a difference to be perceived and k is a constant known as the Weber fraction. Thus, results from humans are compatible with the error in perception of a stimulus increasing with its magnitude as assumed by Reboreda & Kacelnik. There is an extensive literature showing that Weber's Law applies to memory for time intervals (see Fig. 1), but there has been rather less work on amount. Killeen et al. (1993) showed that Weber's Law applies to the discrimination of simultaneously presented seeds of different sizes by pigeons, *Columba livia*; however, it remains to be demonstrated that Weber's Law applies to animals' memories for size or any other index of amount. This is crucial in the context of optimality models, since animals are frequently assumed to make decisions on the basis of their remembered profitabilities of alternatives. Although some models of choice behaviour have incorporated Weber's Law in memory for time (Gibbon et al. 1988; Brunner et al. 1994), Reboreda & Kacelnik (1991) were among the first to consider the impact of Weber's Law in memory for amount on the choices made by animals.

Rationale and Predictions

Our aim in this paper is to test whether Weber's Law might apply to starlings' memories for amounts of food. To do this we used a procedure in which birds were repeatedly required to choose between two foraging options that were cued by different coloured lights. One of these options provided a standard amount of food that remained fixed throughout the experiment. In the other option the amount delivered was adjusted according to the choices made by the bird, getting larger if it preferred the standard, smaller if it preferred the adjusting option and remaining the same if it chose both equally. Based on the assumption that, other things being equal, a foraging bird will prefer a larger amount of food, the accuracy of its estimates will be reflected in the variation in the size of the adjusting option. If estimates are very accurate the adjusting option should remain very similar in value to the standard, since whenever the adjusting option is larger than the standard by more than the JND the bird will choose the adjusting option, resulting in a reduction in its future size towards that of the standard. Similarly, when the adjusting option is more than a JND smaller than the standard the bird will choose the standard resulting in an increase in the future size of the adjusting option. The predicted mean value, or indifference point, of the adjusting option is thus equal to the value of the standard. If error in estimation of amount conforms to Weber's Law, then this should be reflected in the variation in the value of the adjusting option. As the size of the value of the standard option is increased the range of variation in the value of the adjusting option should also increase because discrimination between larger rewards should be less accurate. Therefore, Weber's Law predicts that the variation in the value of the adjusting option should be positively related to the size of the standard reward.

For a given standard size Reboreda & Kacelnik's model of the effects of Weber's Law on memory for amount can be developed to make predictions at a molecular level (i.e. at the level of individual choices) about how the probability of choosing the option offering more food should change as a function of the current value of the adjusting option. If we assume that the memories for the standard and adjusting options are represented as normal distributions centred on the current values of the two options, and that an animal makes choices by randomly sampling from these distributions, then as the difference between the standard and adjusting options increases the probability of making a correct choice (i.e. choosing the option offering more food) should also increase. This occurs because the two distributions overlap less as their means become more different.

To formalize this argument we start by assuming that the memory for the standard option is represented by a normal distribution with mean μ_s (equal to the latest value of the standard option) and standard deviation σ_s and the adjusting option by a normal distribution with mean μ_a (equal to the current real value of the adjusting option) and standard deviation σ_a (this latter assumption is considered further in the discussion). If $\mu_a > \mu_s$, then the probability of making a correct choice is equal to the probability that a random sample, X_a, taken from the adjusting memory is greater than one taken from the standard memory, X_s, i.e. Prob(correct choice) = Prob($X_a > X_s$). Thus, if we define X as $X_a - X_s$, then the probability of making a correct choice becomes equal to the probability that $X > 0$. Since X is normally distributed with mean $X_a - X_s$ and standard deviation $\sqrt{(\sigma^2_s + \sigma^2_a)}$, we have,

$$\text{Prob}(X > 0) = \Phi[z]$$

where $\Phi[z]$ is the standard cumulative normal distribution function, and

$$z = \frac{0 - (\mu_s - \mu_a)}{\sqrt{(\sigma^2_s + \sigma^2_a)}}$$

Reboreda & Kacelnik's model assumes that the standard deviation is proportional to the mean in

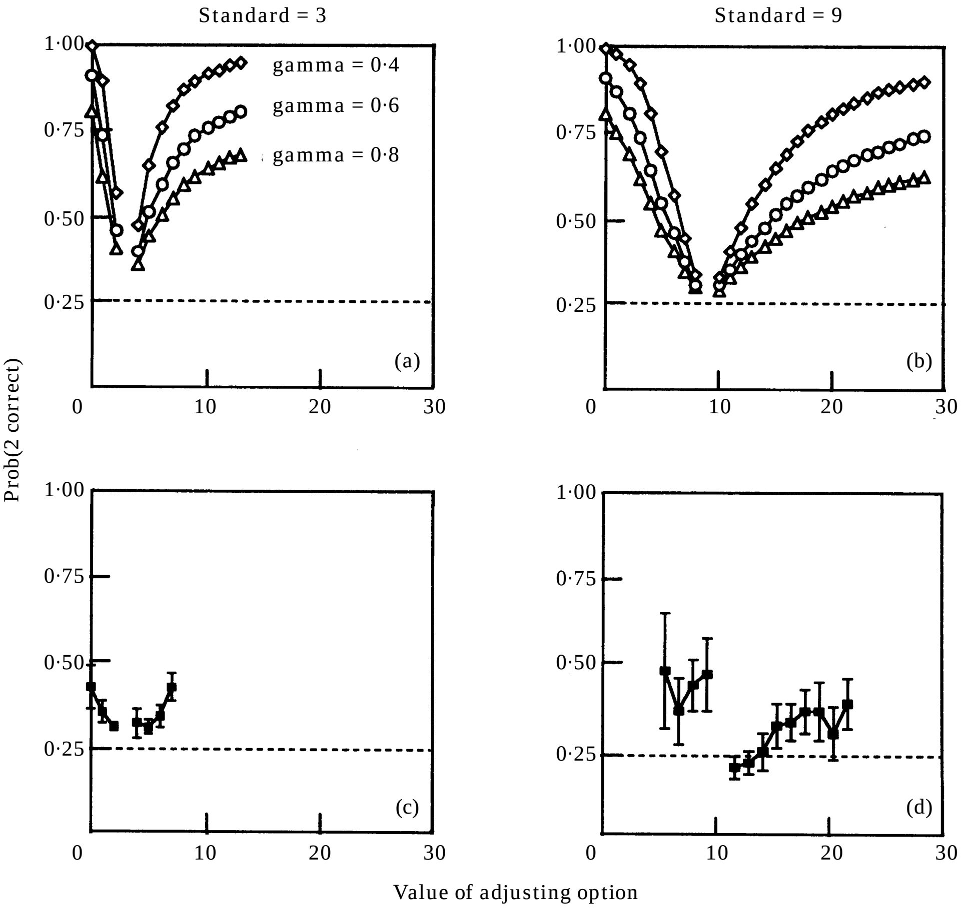

Figure 2. (a, b) Predicted probabilities of making two successive correct choices as a function of the value of the adjusting option. In (a) the standard option equals 3, and in (b) the standard option equals 9. The horizontal dotted lines indicate random choice (if choosing either option is equally probable, then the probability of choosing one of the options twice in succession is 0·5 × 0·5 which is equal to 0·25). (c, d) The observed probabilities of making two correct choices as a function of the value of the adjusting option for (c) a standard size of 3 units of food, and (d) a standard size of 9 units of food. The data are the $\bar{X} \pm$ SEM of the probabilities for six birds in (c) and five birds in (d). The dotted horizontal lines show the expectation if the birds are choosing randomly.

these memory distributions, i.e. the coefficient of variation, γ, is a constant. Since $\gamma = \sigma/\mu$, z can be rewritten as,

$$z = \frac{\mu_a - \mu_s}{\sqrt{[(\gamma\mu_a)^2 + (\gamma\mu_s)^2]}}$$

Using similar reasoning it is possible to show that when $\mu_a < \mu_s$,

$$\text{Prob(correct choice)} = \text{Prob}(X_a < X_s) = \Phi[z]$$

where,

$$z = \frac{\mu_s - \mu_a}{\sqrt{[(\gamma\mu_a)^2 + (\gamma\mu_s)^2]}}$$

In the titration procedure that we employ (see Methods), the value of the adjusting option changes only if the bird makes two consecutive choices for the same option. Since the probability of two choices for the same option is the product of the probability of each choice, we squared the probabilities obtained above and plotted the resulting probabilities as a function of the value of

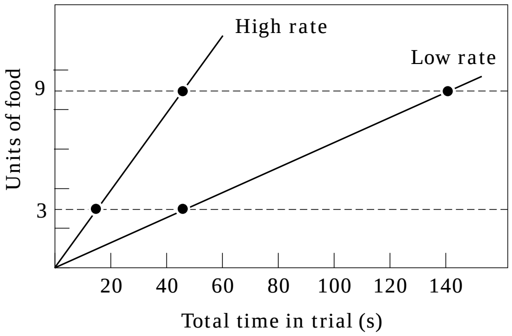

Figure 3. The four treatment combinations (●). The total time in the trial includes the inter-trial interval (ITI), 1 s of estimated latency to peck, 5 s of delay and either 3 or 9 s of reward delivery time. The two different rates were generated by varying the length of the ITI.

the adjusting option for a range of realistic values of γ (Fig. 2a, b). The asymmetry in the shape of these functions about the value of the standard option is due to the constant coefficient of variation, and is therefore a diagnostic prediction of Weber's Law in memory for amount.

A potential problem of testing discrimination with standards of different sizes is that birds receiving more food may be less motivated. To overcome this problem we used a factorial design with two main treatments: the size of the standard reward (Standard), and the overall rate of food delivery (Rate), determined jointly by the reward size and length of each trial. There were two standard sizes, a small standard of 3 units of food and a large standard of 9 units, and two rates of intake, a low rate of 0·06 units/s and a high rate of 0·16 units/s (Fig. 3). Delivery rates were calculated by dividing the units of food available in the standard option by the sum of all of the time intervals in the trial, i.e. the inter-trial interval (ITI), the latency to peck, a 5-s delay to reward and the time taken to deliver the reward. Since the latency is controlled by the bird, for the purposes of these calculations it was assigned a plausible length of 1 s.

METHODS

Subjects

The subjects were 12 wild-caught starlings housed in individual experimental cages (120 × 50 × 60 cm) in an unheated laboratory. The light cycle was 13:11 h light:dark (dark between 1900 and 0600 hours). The temperature in the laboratory fluctuated between 8 and 13°C over the course of the experiment. During training and the experiment the birds were food deprived from 1700 hours until the start of the first session at 0800 hours the following morning. During the experimental sessions the birds were rewarded with sieved turkey starter crumbs, and after the session the birds were given about four mealworms and ad libitum turkey crumbs for the remainder of the day. This regime resulted in the birds being maintained at approximately 90% of their ad libitum feeding weights. After the experiment the birds were kept for future use.

Apparatus

The experiments were conducted in the house cages. Each cage had a panel in the centre of the back wall which had two response keys (3·5 cm in diameter), one on each side of a central food hopper. The keys could be illuminated with either yellow, red or green light. The food hopper was connected to a pellet dispenser (Campden Instruments, Loughborough, U.K.) which was filled with turkey crumbs sieved to an even size. One unit of crumbs had a mean weight of 0·012 g. A BBC Master microcomputer running SPIDER experimental control language (Paul Fray, Cambridge, U.K.) controlled the stimulus events and response contingencies as well as recording the data.

Pre-training

We first trained the birds to ensure that they could learn to discriminate between 3 and 9 units of food. Coloured lights on the pecking keys were used as the discriminative stimuli indicating the two options. For each bird, either the 3 unit option was cued by a green light and the 9 unit option by a red light or vice versa, such that the assignment of colours to options was balanced across birds. The birds had previous experience of pecking illuminated keys for food, therefore no key-pecking training was required.

We used a discrete-trials procedure. There were two types of trials, 'forced' trials and 'choice' trials. The forced trials allowed the birds to experience the two options and learn about their characteristics, and the choice trials tested the

Table I. The assignment of birds to treatment combinations showing the inter-trial interval (ITI) used in each

Rate of delivery (units/s)	Standard (units)	
	Small: 3	Large: 9
Low: 0·06	ITI = 40 s Birds 2, 3 and 10	ITI = 132 s Birds 1, 5 and 6
High: 0·16	ITI = 9·33 s Birds 4, 8 and 9	ITI = 40 s Birds 0, 7 and 11

birds' preferences. A forced trial began with one of the key lights flashing (on for 0·7 s and off for 0·3 s). When the bird pecked the key the light changed from flashing to being continuously on, and a 5-s delay to receive the associated reward began. The first peck after this delay had timed out extinguished the key light and caused the delivery of food to the hopper. Each unit of food took 1 s to deliver. The ITI started to time when food delivery was complete. The ITIs used during training were the same as those used in the main experiment, and thus varied between conditions (see Table I and below). The choice trials were identical to the forced trials except that a trial began with both keys flashing, one in each colour, and as soon as the bird pecked one of the keys this one was illuminated continuously and the other was extinguished.

All the birds were given daily sessions of 12 blocks. A 'block' consisted of eight forced trials followed by two choice trials. The eight forced trials included four of each option given in a different randomly chosen order for each block. Half of the trials of each type appeared on the left key, and the other half on the right. This procedure was designed to prevent side preferences from developing, and to ensure that the birds had experienced both options an equal number of times before having to choose between them. When a bird had completed a session, generally between 1200 and 1500 hours, it was given ad libitum food until 1700 hours when all of the birds were deprived for the night. The criterion for stopping this training was when a bird had, for 2 consecutive days, showed a 70% or greater preference in the choice trials for the 9 unit option.

Titrations

For each bird, one of the two options experienced during training became the standard option which remained unchanged over the course of the experiment. The other became the adjusting option. Table I summarizes the assignment of birds to treatment combinations. Following on from training, the birds in the small standard treatment started with the adjusting option delivering 9 units, and the birds in the large standard treatment started with the adjusting option delivering 3 units. To control for colour preferences, in each standard size three birds had red associated with the standard option, and the other three had red associated with the adjusting option.

The details of the schedules and the sequence of forced and choice trials used were identical to training, but now the value of the adjusting option was programmed to alter after each pair of choice trials as follows. If a bird chose the standard option twice in a pair of choice trials then the adjusting reward became 1 unit larger, if a bird chose the adjusting option twice it became 1 unit smaller, and if a bird chose each option once then no change followed. The birds could experience a maximum of 12 blocks in a day, but if they had not completed this number by 1500 hours the session ended. Each new session began with the adjusting option set at the value at which it finished in the previous session. Birds experienced at least 270 blocks with the exception of bird 5 which was removed from the experiment after only 83 blocks because the value of the adjusting option failed to stabilize. As a consequence of the different amounts of food the birds were receiving there was some variation in the number of trials they completed each day (see Table II for means).

Analysis

Throughout these titrations the dependent variable of interest was the value of the adjusting option that was recorded in every block. Since visual inspection of these data did not show overall differences between the beginning and later periods of the experiment, we used all of the titration data in the analyses. The variation in the value of the adjusting option was measured in two ways: (1) as the standard deviation of all of the values taken by the adjusting option, and (2) as the average number of blocks occuring between blocks in which the adjusting option was equal to the value of the standard, calculated by dividing the total number of blocks completed by the number of times that the adjusting option was

Table II. The mean value of the adjusting option, the total number of blocks and the mean blocks per session for each of the birds

Small standard				Large standard			
Bird	Mean value of adjusting option	Total number of blocks	Mean blocks per session	Bird	Mean value of adjusting option	Total number of blocks	Mean blocks per session
2	4·51	329	11·00	0	10·27	355	9·91
3	3·61	418	11·94	1	16·16	364	10·11
4	4·23	348	12·00	5	28·69	83	6·00
8	4·03	396	12·00	6	9·99	312	9·46
9	3·87	372	12·00	7	10·10	312	9·75
10	3·54	384	12·00	11	13·99	270	8·25
Mean	3·97			Mean	12·10*		

*This overall mean excludes the value for bird 5 which failed to stabilize.

equal to the standard option. We refer to this as the ‘period’ of the oscillations. This second measure is not independent of the standard deviation, because the size of the step in the adjusting option is constant so constraining the period to increase as the amplitude of the oscillations increases.

To test the molecular predictions outlined above, we estimated the probability of making a pair of correct choices as a function of the value of the adjusting option. The data were pooled for all the birds in a treatment in order to achieve reasonable sample sizes. We calculated the proportion of occasions on which a bird made a pair of correct choices for each value of the adjusting option. If a bird made a random and totally independent choice on each of the two choice trials, then the expected value of this proportion is 0·25.

RESULTS

After a number of pre-training sessions ($\bar{X} \pm$ SD$=4{\cdot}25 \pm 3{\cdot}25$) all 12 birds showed a significant preference for the 9 unit option over the 3 unit option and were switched to titration.

In all of the birds, apart from bird 5, the value of the adjusting option oscillated around the value of the standard option. Table II shows the mean value of the adjusting option for each bird (overall means are given in Fig. 4a). These means are on average approximately 33% larger than the standard. This bias towards the standard is significant given that it was seen in all 12 birds (sign test: $N=12$, $P<0{\cdot}001$).

The consequences of Weber’s Law can be illustrated most clearly by plotting the frequency with which the adjusting option took each value in the two standard size treatments (Fig. 5). When standardized relative to the value of the standard option on the X-axis, and relative to the frequency with which the adjusting option is equal to the standard option on the Y-axis, these two distributions superimpose showing that relative accuracy is constant (Fig. 6).

Figure 4b shows the standard deviations of the value of the adjusting option in the different treatment combinations. A two-way ANOVA on the standard deviations shows that Standard has a significant effect on the standard deviation ($F_{1,8}=34{\cdot}54$, $P<0{\cdot}001$), but neither the Rate nor the interaction of Standard and Rate is significant ($F_{1,8}=0{\cdot}73$, $P=0{\cdot}418$ and $F_{1,8}=0{\cdot}04$, $P=0{\cdot}854$, respectively). This analysis was performed on the reciprocals of the standard deviations in order to stabilize the variance of the residuals. Bird 5 (which did not stabilize) is included in this and all subsequent ANOVAs on the grounds that its behaviour was probably not independent of the treatment combination it experienced. We did, however, repeat the analyses excluding bird 5, and the results were not qualitatively different.

Weber’s Law states that the relative error in measurement should be equal in the small and large standard conditions. Figure 4d shows the coefficient of variation for each bird calculated by dividing the standard deviations by the mean value for each bird. A two-way ANOVA on this relative measure shows that neither Standard nor Rate nor their interaction explains a significant

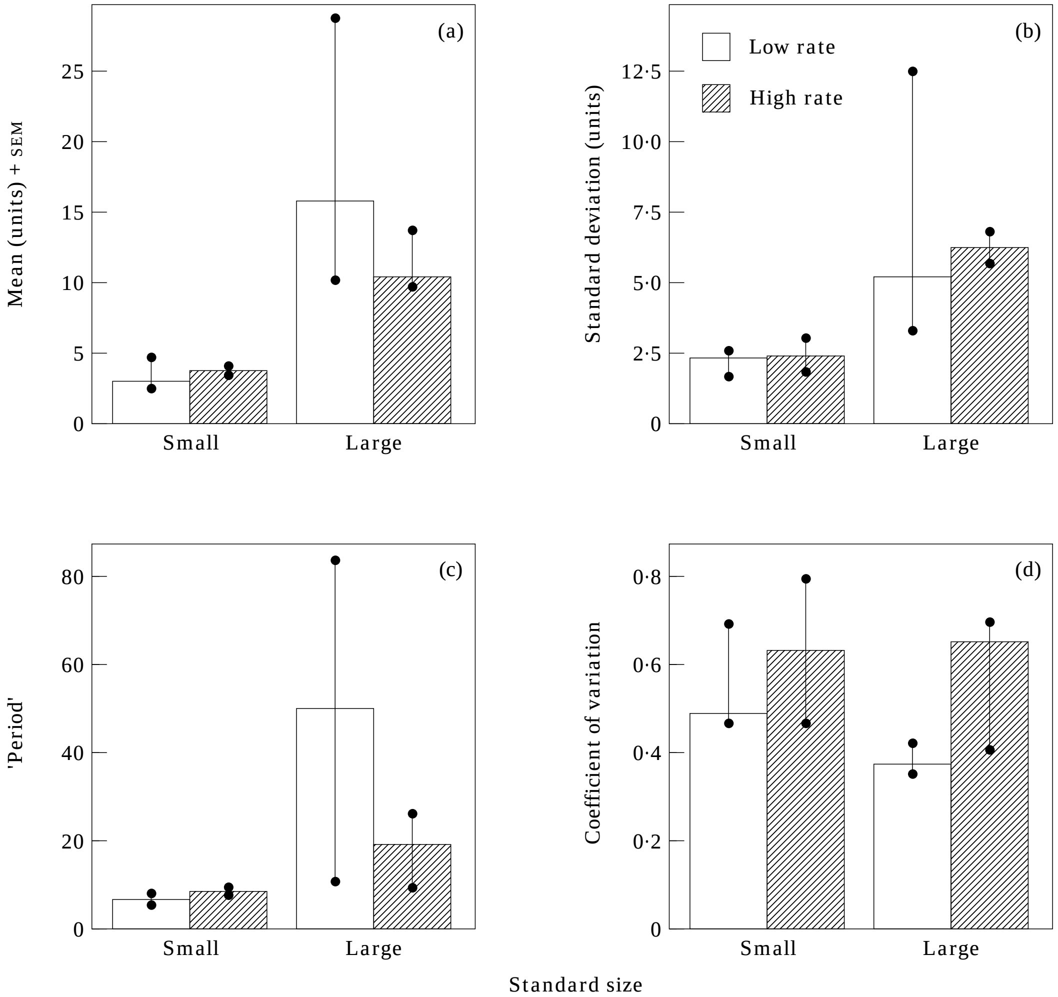

Figure 4. (a) The mean values of the adjusting option in the four treatment combinations, (b) the standard deviations, (c) the periods (i.e. the average number of blocks occurring between blocks in which the adjusting option was equal to the standard option) and (d) the coefficients of variation. Data from three birds contribute to each bar: the bar itself is the median value and the filled circles indicate the other two data points.

amount of the variance in the coefficient of variation ($F_{1,8}=4{\cdot}55$, $P=0{\cdot}065$; $F_{1,8}=4{\cdot}18$, $P=0{\cdot}075$ and $F_{1,8}=2{\cdot}20$, $P=0{\cdot}177$, respectively). In this case it was necessary to log-transform the coefficients of variation in order to stabilize the variance of the residuals.

Figure 4c shows the periods of the oscillations in the different treatment combinations. A two-way ANOVA on the period scores for each bird shows that Standard has a significant effect on period ($F_{1,8}=23{\cdot}91$, $P<0{\cdot}001$), but neither Rate nor the interaction between Rate and Standard explains a significant amount of the variance ($F_{1,8}=0{\cdot}02$, $P=0{\cdot}887$ and $F_{1,8}=1{\cdot}86$, $P=0{\cdot}210$, respectively). Here a reciprocal transformation of the period scores was used to stabilize the variance of the residuals.

Molecular Results

Figure 2c, d shows the mean proportion of times the birds made two correct choices at each value of the adjusting option. Probabilities are plotted only for values of the adjusting option for

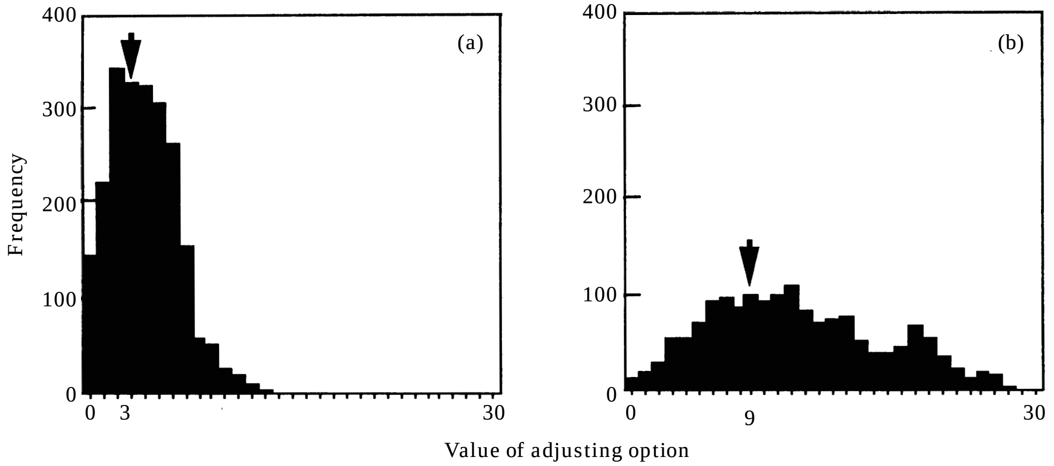

Figure 5. Pooled frequency distributions showing the number of times the adjusting option was at different values when (a) the standard was 3 units of food, and (b) the standard was 9 units of food. (a) Data from birds 2, 3, 4, 8, 9 and 10 and (b) birds 0, 1, 6, 7 and 11.

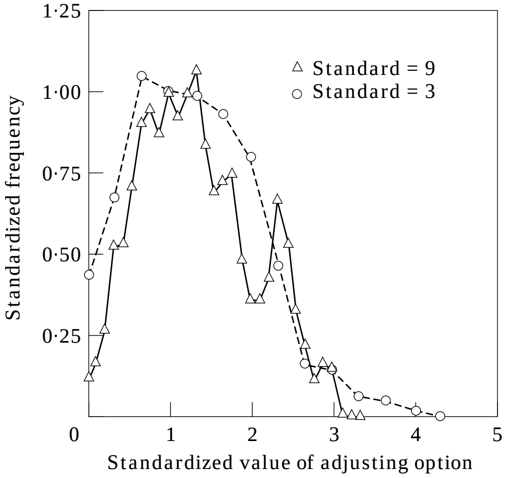

Figure 6. Standardization of Fig. 5 to show superposition.

which there were sufficient data for all of the birds. The criterion was that for each bird the number of data points from which the proportion was calculated had to be greater than or equal to 10 in Fig. 2c and greater than or equal to 2 in Fig. 2d since the sample size falls for values of the adjusting option distant from the value of the standard. The observed functions differ from the model's molecular predictions, but for both standard sizes there is some indication of the V-shaped function about the value of the standard as shown in Fig. 2a, b: in both treatments the probability of two correct choices approaches random when the value of the adjusting option is very close to that of the standard, and rises either side of this point. The data also show the predicted asymmetry, with the probability of making two correct choices increasing more steeply to the left of the standard than to the right in both treatments, although the effect is more pronounced in Fig. 2d.

DISCUSSION

Our aim in this study was to seek evidence for the relevance of Weber's Law to birds' memories for amounts of food. To do this we used a titration procedure in which starlings repeatedly chose between two stimuli that had been paired with differently sized food rewards. One of the options had a fixed, standard value, and the other adjusted according to the choices of the birds, decreasing when they chose it and increasing when they chose the standard. Schedules of this type have previously been used for obtaining indifference points between two options which are estimated as the mean or median of the values taken by the adjusting option (Lea 1976; Mazur 1984; Wogar et al. 1992; Bateson 1993). Here we focus on the variation in the value of the adjusting option as a measure of estimation error, and therefore as a means to test for Weber's Law.

The assumption that variation in the accuracy of choice reveals variability in memory needs some justification since other sources of variation can be invoked. For example, some degree of variation is inevitable as a result of the way the titration procedure is programmed because the computer program's decision about whether to change the value of the adjusting option used the outcome of only two choice trials. If the subject were indifferent between the two options and chose randomly, it would have a 50% chance of picking either the standard or the adjusting option twice consecutively, and thus causing the value of the adjusting option to change by one step in the following block of forced trials. This effect alone, however, cannot account for the variation observed, because it would cause the value of the adjusting option to move only one step in either direction away from the value of the standard, producing no differences between treatments. Similarly, proactive interference from the memory formed of the value of the adjusting option in previous blocks may also explain why a subject does not choose the currently larger of the two options. This phenomenon may add variation to the data, but again it does not predict differences in the degree of variation observed between treatments. Thus, although factors other than just discrimination error will contribute to the variation in the value of the adjusting option, only perceptual, memory and decision processes subject to Weber's Law predict variation that varies between treatments with different standard sizes.

An initial period of training demonstrated that the birds could discriminate cues associated with 3 and 9 units of food, and that they preferred the cues associated with larger rewards, thus confirming the main assumptions underlying the titration procedure. The results from the titrations can be summarized as follows. The value of the adjusting option oscillated around a mean value that was similar to, but always larger than the standard. The oscillations in the value of the adjusting option had both a larger 'period' and a larger standard deviation with a standard of 9 units than with a standard of 3 units. Consistent with Weber's Law, when the standard deviation is expressed as a ratio relative to the value of the standard the birds show similar accuracy at both standard sizes. Furthermore, when the distributions of values taken by the adjusting option are standardized relative to the value of the standard and the frequency with which the adjusting option equalled the standard, the resulting distributions for the two standard size conditions superimpose. This suggests that accuracy is constant on a relative scale. An analysis of individual choices shows that, as the difference between two rewards increases, the probability that a bird will choose the larger option also increases. The shapes of the observed functions are asymmetrical in agreement with the molecular predictions we derived from Scalar Expectancy Theory (SET), the theoretical framework based on Weber's Law described in the Introduction.

A striking feature of our results is that the mean value of the adjusting option is always higher than the value of the standard. This implies that the birds were biased against the adjusting option, because the adjusting option had to give more food to be equally liked. Simple explanations for a bias such as colour or side preferences can be excluded since colour and side were balanced between birds and trials, respectively. We consider three possible explanations for this bias.

(1) Molar versus molecular maximization. The titration algorithm involved blocks consisting of eight forced trials followed by two choice trials, and therefore overall reward rate is affected by the rewards received in both forced and choice trials. Choices have two effects: the immediate consequence of the current choice and the delayed effect of any resulting change in the value of the adjusting option. Consider the average reward sizes of two hypothetical choice strategies, molar and molecular maximizers, where a molar maximizer is defined as choosing options so as to maximize the average size of reward, and a molecular maximizer is defined as always choosing the currently larger of the two options. The total amount of food delivered in a block is equal to $4S+4A+C_1+C_2$, where S is the value of the standard, A is the current value of the adjusting option and C_1 and C_2 are the amounts earned in the first and second choice trials (either S or A). Owing to our titration schedule, a molecular maximizer that chooses the larger option in both of its choices will drive A towards the value of the standard, and its average reward will therefore be 10S. A molar maximizer instead always chooses the standard, obtaining $6S+4A$ per block. Although $2(A-S)$ is lost in the choices, this is more than compensated for by A being driven to

ever increasing values. Thus, the strategy of molar maximization is to avoid the 'temptation' of an immediate larger reward in order to drive up the size of later rewards. Evidence from studies of self control (reviewed in Logue 1988) and from frequency-dependent schedules (Vaughan & Herrnstein 1986) suggests that this is a very unlikely result. However, we cannot exclude the possibility that a tendency towards molar maximization produced the bias against the adjustable option and perhaps caused the runaway increase in the adjusting option for bird 5. Similar results were also sometimes obtained in titrations with amount by Bateson (1993). It should be noted that the above calculations are based solely on reward size, when of course what is important for optimal foraging theory is rate of intake. Larger rewards take proportionately longer to deliver, but given the constant and relatively long time component in each trial caused by the inter-trial interval and delay, which are independent of amount, the size of rewards will generally control the overall rate of delivery.

(2) Asymmetric effect of Weber's Law. According to Weber's Law, a difference when the adjustable option is smaller than the standard is more discriminable than the same difference in the opposite direction. Therefore the value of the standard will be recovered more quickly when the adjusting option is lower in value than the standard than when it is higher in value. Hence, a molecular maximizer subject to Weber's Law would show asymmetrical oscillations, and consequently this strategy also predicts that the adjusting option will have a mean higher than the standard.

(3) Memory updating. We have assumed that at the time of a choice the memory for the adjusting option is equivalent to the memory for a fixed reward with the current value of the adjusting option. This value is given to the subject in the forced trials preceding choice in each block. However, memory for the adjusting option may be affected by values taken by this option in the past, and it may therefore share properties with the memory for variable rather than for fixed rewards. Todd & Kacelnik (1993) proposed a dynamic model of memory updating that would produce this effect, and Bateson (1993) developed a related dynamic model for a paradigm such as the present one. If memory for the adjustable option shares properties with that for variable rewards, accounts in terms of reward variability may produce the observed bias. The usual result in studies of preference between fixed and variable rewards is aversion to variability in amount (Real 1981; Waddington et al. 1981; Hamm & Shettleworth 1987; Wunderle et al. 1987; Barkan 1990; Clements 1990; Tuttle et al. 1990), either because of an intrinsically decelerated increase in the utility of amount (Real 1991) or for the mechanistic reasons based on Weber's Law given by Reboreda & Kacelnik (1991) and by Bateson & Kacelnik (in press).

Note that although Weber's Law is involved in both cases, the accounts under (2) and (3) are different, because the asymmetric effect of Weber's Law is not dependent on considerations of variability. The two accounts can be separated experimentally as follows. The pseudo-variability induced by memory updating should decrease if the number of forced trials preceding choice in each block is increased, allowing choices to be based on longer periods of stable samples of the adjustable option. To our knowledge, there are no independent tests of the effect of varying this dimension. However, in titrations of delay to reward using pigeons Lea (1976, test series 1) found no bias using a schedule without forced trials, whereas Mazur (1984) obtained values of the adjustable option 15% larger than those of the standard using four forced trials. This difference between studies apparently opposes our prediction based on account (3). Lea's experiment, however, also differed from both Mazur's and ours in that he used geometric adjustments in the titration procedure, in which the size of the step was proportional to the current value of the adjusting option. Geometric adjustment maintains the discriminability of each step and thus could affect the asymmetry predicted by account (2).

Our findings have implications for all theoretical models of foraging behaviour that make assumption about animals' memories for quantities of food. For instance, Yoccoz et al. (1993) considered errors in estimation of both gain and time to be independent of the magnitude of the quantity being estimated. Experiments on starlings, however, have shown that for both time (Brunner et al. 1992), and now amount, this assumption is incorrect. A modified version of this model needs to be analysed if it is to be worth testing in the ways that Yoccoz et al. suggested. In accord with our experimental results, Reboreda &

Kacelnik's (1991) model assumes proportional error in memories for both amount and time. The model builds on the basic version of Weber's Law by adding specific assumptions about the way in which memories are represented and retrieved. The sampling process by which information is retrieved from memory introduces the probabilistic element that is characteristic of most discrimination data. The value of the SET framework can be seen in its application to modelling a range of timing problems in behavioural ecology including optimal sampling frequencies (Shettleworth et al. 1988) and patch residence time (Brunner et al. 1992; Todd & Kacelnik 1993). Our results give weight to Reboreda & Kacelnik's (1991) claim that a similar framework may be applicable to problems concerning memory for amount.

One issue not addressed in this experiment is the mechanism used by the starlings to assess amounts. Schuler (1990) has argued that starlings are capable of measuring the calorific value of different food sources using post-intestinal effects. Such a mechanism does not seem plausible here, however, since with a maximum inter-trial interval of 132 s the two options would have been experienced too close together in time to result in attributable blood sugar differences. Therefore the birds must have been using some more immediate estimate of calorific value. A variety of possible mechanisms have been proposed in other species. For example: pigeons and chicks, *Gallus gallus domesticus*, prefer, or learn faster about, options that offer more consummatory activity even if the actual amount of food gained is the same (Wolfe & Kaplon 1941; Shettleworth 1985); piñon jays, *Gymnorhinus cyanocephalus*, use bill-weighing to identify heavier seeds that contain an endosperm (Ligon & Martin 1974); and shore crabs, *Caranus maenas*, measure the dimensions and perhaps also weight of mussels, *Mytilus adulis*, by handling them in their chelae (Elner & Hughes 1978). In our experiment the time taken to deliver a reward, the time taken to consume it, its weight and the number of crumbs it contained were all directly proportional to its calorific content, meaning that the birds could have been using any of these cues to assess the value of a reward. From the point of view of modelling the effects of estimation error, however, the exact mechanism of measurement is irrelevant; what matters is the proportional nature of the error.

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