

## Sequential and simultaneous choices: Testing the diet selection and sequential choice models

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### ABSTRACT

We investigate simultaneous and sequential choices in starlings, using Charnov's Diet Choice Model (DCM) and Shapiro, Siller and Kacelnik's Sequential Choice Model (SCM) to integrate function and mechanism. During a training phase, starlings encountered one food-related option per trial (*A*, *B* or *R*) in random sequence and with equal probability. *A* and *B* delivered food rewards after programmed delays (shorter for *A*), while *R* ('rejection') moved directly to the next trial without reward. In this phase we measured latencies to respond. In a later, choice, phase, birds encountered the pairs *A*–*B*, *A*–*R* and *B*–*R*, the first implementing a simultaneous choice and the second and third sequential choices. The DCM predicts when *R* should be chosen to maximize intake rate, and SCM uses latencies of the training phase to predict choices between any pair of options in the choice phase. The predictions of both models coincided, and both successfully predicted the birds' preferences. The DCM does not deal with partial preferences, while the SCM does, and experimental results were strongly correlated to this model's predictions. We believe that the SCM may expose a very general mechanism of animal choice, and that its wider domain of success reflects the greater ecological significance of sequential over simultaneous choices.

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We examine the classic diet choice foraging problem (Charnov, 1976) from the joint perspectives of rate maximization and causal control. These two viewpoints reflect function and mechanism, two of Niko Tinbergen's four levels of analysis (Tinbergen, 1963). Although framed in theoretical ideas, our study was triggered by a recent empirical finding. Shapiro et al. (2008) reported that the choices of European starlings, *Sturnus vulgaris*, between simultaneously available food sources could be precisely predicted from the way the birds behaved towards each source when found alone. In their experiment, when birds found a food source in isolation (as in experimental no-choice, or forced, trials), they did not respond to it immediately, but instead showed a delay of a few seconds, or 'latency' before doing so. The frequency distribution of these latencies was affected by the properties of the food source in front of the animal and by the background opportunities in the environmental context: latencies were shorter when the present option was richer and when alternative sources in the environment were poorer. Shapiro et al. (2008) encapsulated these results in a theoretical model that, for reasons that will become clearer below, they called the sequential choice model (SCM). The reason SCM is significant in a foraging context is that the phenomenon provides a

link between two important theoretical paradigms (and possibly many others): choice in simultaneous encounters and prey choice in sequential situations (see Stephens and Krebs, 1986). Shapiro et al. suggested that SCM may offer a simple mechanism for adaptive behavior in many foraging paradigms. In the case of simultaneous choice where two food sources are simultaneously present, the subject as modeled by SCM 'chooses' without an on-the-spot comparative evaluation: by letting each food source express the latency it would have when being alone, it attacks the source that elicits the shorter latency, and the alternative is ignored for that opportunity. SCM thus leads to partial preferences that favor the richer option to different degrees depending on the relative values of the environmental opportunities. As in the case of the matching law (e.g., see Herrnstein, 1970, 1990), this is a prediction that will often clash with functionally predicted rate maximization.

When foraging opportunities are encountered one at a time, rather than simultaneously, Charnov (1976) identified the treatments under which a greater overall rate of gain would be achieved by rejecting poorer prey to continue searching for more profitable types (specialist strategy) than by accepting all the prey encountered (generalist strategy). According to Charnov's model, a prey's profitability (i.e., the ratio of its energy content to its involvement time) and its associated opportunity cost (i.e., the rate of energy return of the environment as a whole multiplied by the handling time) are the main elements that an ideal animal should consider to maximize rate of return (see also Stephens and Krebs, 1986; Houston and McNamara, 1999, p. 20).

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Charnov's profitability, which in many schedules of reinforcement is represented by the ratio of amount of reward to the delay between the choosing response and the end of that reward's consumption, also plays a major role in descriptive models of choice originating within the behavioral analysis tradition. Shapiro et al. (2008) argued that the latency mechanism could be ideally designed to implement rate-maximizing strategies in sequential choice situations such as those envisaged by Charnov. An animal's latency to accept an option in an experimental cage may well be correlated with the animal's likelihood of not consuming the prey in the wild. This could work either as a passive selective rejection mechanism (the chances of the consumer being distracted or the prey escaping increase during a longer latency) or as an active rejection, if a free-living consumer would actually abandon the site with greater probability during a longer latency. This possibility is underlined by the fact that latency responds appropriately to both the ratio of amount to delay and the background rate of gain, both variables at the centre of Charnov's prey selection model.

## 1. The experiment

We used a procedure derived from early laboratory implementations of the diet choice problem by Krebs and collaborators (1977) and by Lea (1979). In the training phase, each trial consisted of an initial 'search' period, after which subjects faced only one among three possible stimuli. Two of these stimuli (*A* and *B*) were paired to a direct feeding reward with a characteristic delay between the bird's response and food delivery. The third (*R*) was a 'rejection' key. Responding to *R* led to no reward in that trial, but to the initiation of a new trial where again, any of the three stimuli could appear with equal probability. During this training phase birds developed a characteristic latency to peck at each of the stimuli. After around 300 training trials, the choice phase started. In the choice phase, two of the three stimuli appeared in each trial, offering a choice of *A* vs. *R*, *B* vs. *R*, or *A* vs. *B*. The two first pairings implement 'sequential' choices, as the subjects choose whether to accept the reward (by pecking *A* or *B*) or abort the trial (by pecking *R*). Subjects experienced five within-subject treatments in which option *A* was unmodified, at 1 s delay to food, while option *B*'s delay was either 4 s, 8 s, 12 s, 16.8 s, or 24 s, on treatments 1–5, respectively. These parameters were chosen by reference to Charnov's (1976) diet choice model, that compares the rate of intake of a generalist that always chooses *A* over *R* and *B* over *R*, against that of a specialist, that chooses *A* over *R* but *R* over *B* (see details in Appendix A). According to this model, the theoretical intake gain of a generalist respect to that of a specialist would be +50%, +20%, 0%, –20% and –50% for our parameters in treatments 1–5, respectively. Thus, rate of gain would be maximized by choosing *A* over either *B* or *R*, choosing *B* over *R* when *B*'s delay was either 4 or 8 s, and *R* over *B* when *B*'s delay was 16.8 or 24 s (when *B*'s delay was 12 s, the rate of food intake was unaffected by the choice between *B* and *R*).

To bring function and mechanism together we examine the birds' preferences in relation to Charnov's rate-maximizing model, and we test the extent to which SCM provides a mechanism for their choices.

The predictions of the rate maximization model are presented in Appendix A.

## 2. Materials and methods

### 2.1. Subjects

Six wild-caught starlings (under Natural England license 20063260) served as subjects. All subjects had participated in

experiments where pecking at lighted keys was required to obtain food, though present stimuli were unfamiliar to them. Birds were housed in an outdoor aviary and, before the beginning of the experiment, were transferred to indoor individual cages that served as both housing and experimental chambers. These cages were vertically stacked in groups of two in climate controlled rooms maintained at 16 °C ( $\pm 3$  °C). Automatic timers maintained a light/dark cycle of 12:12 h (lights on at 7 a.m., and off at 7 p.m.). Subjects were visually but not acoustically isolated. Fresh drinking water was always available, and bathing pools were provided twice a week on afternoons once the experimental session was over. During experimental sessions, birds worked for BioServ precision pellets. These rewards were supplemented daily after the last experimental session by 3 h of *ad libitum* access to turkey crumbs and supplementary mealworms (*Tenebrio* sp.). This regime allows starlings' body weights to remain stable above 90% of their free feeding values (Bateson, 1993).

The experiment took place in May 2007, and once finished, birds were kept in the colony for further research. Experimental procedures complied with the norms of the local ethical review process at the Zoology Department, University of Oxford.

### 2.2. Apparatus

Starlings were tested individually in their home cages, which were 120 cm long  $\times$  60 cm wide  $\times$  50 cm high, and were equipped with two perches, one at each side of the cage (85 cm apart), and an operant panel with a central food hopper and three circular response keys (3 cm in diameter). Keys could be trans-illuminated in green, red, blue, orange, and white. The hopper had an entrance 4 cm wide  $\times$  3.5 cm high and was illuminated whenever food was delivered. Experimental trials were governed by a Windows PC running the Animal Behavior Environment Test System (Campden Instruments®) for both the control of contingencies and recording of the data. Food rewards were fixed for all schedules at two precision pellets (20 mg, Bio-Serv, USA) delivered at a rate of 1 U/s through an automatic food dispenser (Campden Instruments®).

### 2.3. Procedure

#### 2.3.1. Pretraining

All subjects were pretrained to eat from the hopper and peck at the central and lateral keys to obtain food. For this purpose, the birds experienced a mixed 'autoshaping/fixed interval' schedule, in which food was delivered 8 s after the central key was turned on or earlier if the bird pecked at the lighted key, with an inter-trial interval (ITI) of 50 s. This training continued until starlings showed consistent pecking at the central key to obtain food. The next step was to train the birds in fixed interval (FI) schedules. In this second phase of pretraining, birds experienced three daily sessions in which they had to peck at a flashing color in either lateral key to obtain food according to a progressively longer FI schedule. The FI was 1 s at the beginning of the session, and was progressively increased across trials until it reached a value of 24 s on the few last trials of each session. In each trial the starlings had to peck once at the flashing central key to turn this light permanently on and start a randomly variable interval with a mean of 5.5 s (this component would at a later stage represent the time cost of an active searching period). Once this searching interval lapsed, the central key turned off and one of the lateral keys started flashing. Then, birds had to peck at the laterally flashing color to turn it steadily on and to initiate the corresponding FI; the first peck after the programmed FI elapsed delivered the reward. Pretraining ended when all starlings were reliably pecking at FI 24 s to get food. After pretraining, cues were replaced with novel colors.

### 2.3.2. Training phase

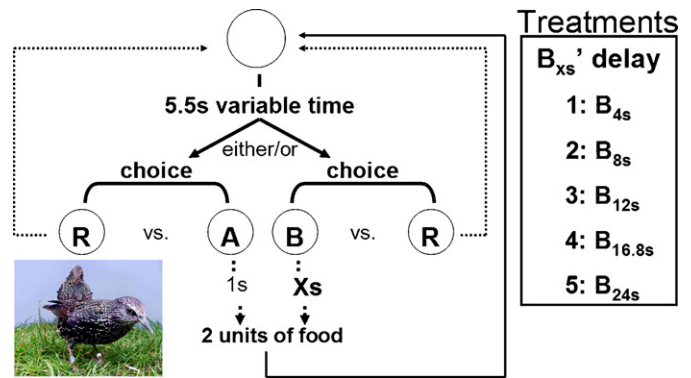
The training phase lasted for three sessions (1 day) in each treatment. Sessions started at 7 a.m., and each session lasted for approximately two and a half hours or 100 rewarded trials, which ever came first. During a training session, birds were exposed to three options signaled by colored cues (i.e., A, B, and R) presented on either lateral key. Only one option was presented per trial, and all options had the same probability of appearing in any particular trial. Sessions consisted of 10 blocks of 10 rewarded trials each. Since a block's length was determined by the number of rewarded trials (i.e., the sum of trials with options A and B), and the presentation of option R occurred with a probability of 1/3, the total number of trials in a session was not fixed. Nonetheless, subjects experienced a similar mean number of trials with options A, B, and R per session (averaging across subjects and treatments, mean number of trials per session  $\pm 1$  S.E.M., option A =  $36.22 \pm 2.73$ , option B =  $36.32 \pm 3.36$ , and option R =  $33.87 \pm 3.29$ ). Each trial came immediately after the previous one (there was no inter-trial-interval or ITI), but blocks were separated by 10-min intervals.

Training sessions consisted of only forced trials, in which one option was presented at a time. Forced trials provide the birds with information about the consequences associated with each colored key. Trials began with the central key flashing (0.7 s on, 0.3 s off). A peck to the central key turned this light steady on and began an exponentially distributed variable interval (representing the 'searching' time) with a mean of 5.5 s. After the interval elapsed a peck turned the central key off, and one of the lateral lights began flashing. Lateral colors were paired to specific delays to food in the case of options A and B, and directly to the searching phase of the next trial in the case of option R. Once the bird pecked at the flashing side key showing option A or B, this side key's light turned steadily on, and the corresponding programmed delay began. The first peck to the same key after the delay elapsed turned its light off, and triggered the delivery of two food pellets, immediately followed by the next trial. If no peck was registered within 5 s of the programmed delay elapsing the trial started again with the same option available. For trials with R, a peck at the flashing light caused all key-lights to turn off and the next trial to start with the central key flashing.

### 2.3.3. Choice phase

This phase began a day after the training phase. Here we introduced two new trial types: sequential and simultaneous choices. Sequential choices consisted of rewarded options paired with the rejection key (A vs. R or B vs. R), while simultaneous choices paired the two rewarded options (A vs. B). Single option (forced) trials were not present in this phase of the experiment. Subjects received these trials in three daily sessions; each session lasted for two and a half hours or 100 rewarded trials (whichever was reached first) arranged in 10 blocks (i.e., five blocks of sequential choices and five blocks of simultaneous choices). While blocks of simultaneous choices always consisted of 10 trials, blocks of sequential choices could contain additional trials because when the animal selected option R (i.e., chose to skip the present reward) this trial did not count towards the 10 rewarded trials that determined block length. Starlings actually experienced a mean ( $\pm 1$  S.E.M.) of 41.49 ( $\pm 3.02$ ) A vs. B choices, 23.08 ( $\pm 2.96$ ) A vs. R choices and 23.42 ( $\pm 3.25$ ) B vs. R choices per session (averaged across treatments). Similarly to the training phase, there was a break of 10 min between consecutive blocks. For each individual bird in each treatment, the choice phase lasted until A vs. R, B vs. R, and A vs. B choices were stable, as indicated by standard deviations of the proportion of choices for the last three sessions being equal or below 0.1, and no upward or downward trend in the data was identifiable.

Like forced trials, choice trials began with the central key flashing, which led to the same randomly variable searching interval (i.e., with a mean of 5.5 s) once pecked. After the variable interval was



**Fig. 1.** Schematic representation of each option's consequence during sequential choices. After pecking at the flashing central light (here represented as an empty circle), a choice trial presented either A vs. R or B vs. R choices. Option A offered a 1-s delay to food in all treatments, while option B was paired with delays of 4 s, 8 s, 12 s, 16.8 s, or 24 s in treatments 1–5, respectively. After food was delivered, the following trial immediately started with the central key flashing. When R (i.e., the rejection key) was pecked, that trial was not reinforced and following trial started immediately. Simultaneous choices, not shown in the figure, offer a choice between A and B.

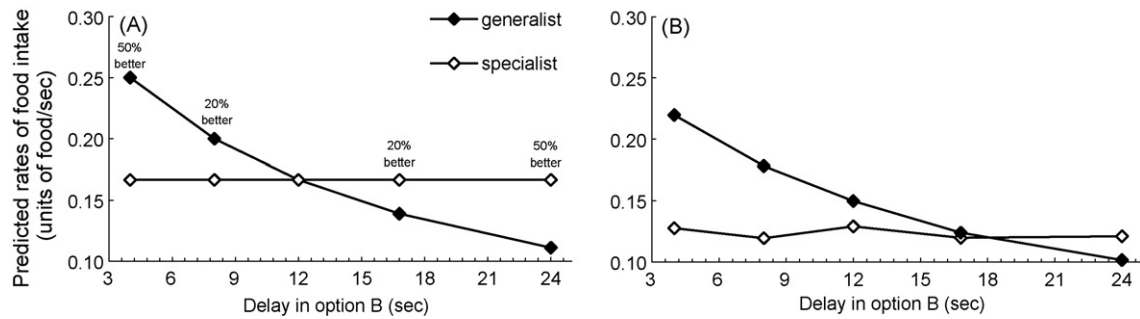
finished, another peck turned the central key off, and two different colors started flashing on either lateral key (options had the same probability of appearing on either side). The first peck to any of the side keys caused the chosen color to turn steadily on in the case of options A and B, and the other key to turn off. The trial continued as in forced trials including the delivery of food when appropriate (i.e., when the subject pecked the active key at least once within a 5-s interval after the programmed delay elapsed). If R was chosen, all key-lights turned off, and the searching component of the next trial started immediately (see Fig. 1 for a schematic representation of each option's consequences during sequential choices).

The main procedural difference between *Lea's sequential choice experiment* (1979) and ours is that in his procedure the initial searching key served also as the key that re-started the foraging cycle, while we used a different key to play that role (see Fig. 1) because a priori it seemed to us that having a key whose sole function was to reject the present option to re-start the searching effort made it easier to identify a specific rejection decision.

### 2.3.4. Experimental treatments

The equations giving the theoretical rates of return of the ideal generalist and specialist strategies are described in *Appendix A*. However, these ideal strategies include the unrealistic assumption of immediate responding. This assumption has a similar theoretical status to that of partial preferences: an ideal maximizing subject under the experimental treatments would not show them, but they are universally present, and furthermore, they are systematic. For these reasons, *Cassini and Kacelnik* (1994) have suggested to include what they called 'recognition time' in the diet and patch choice models. We followed this approach here, formulating a modified diet choice model that includes the programmed delays to reward for each option plus the average delay shown by the animals when responding to such an option in no-choice situations. We return to the justification of this approach in the general discussion. The payoffs of both strategies using the ideal and modified models are shown in Fig. 2A and B, respectively.

For a particular bird in a given treatment, a specific option or color was consistently associated with a given delay to food, while the color of R was consistent throughout for each bird. Colors were however counterbalanced across subjects, and when a bird entered a new treatment, colors associated with options A and B were reversed relative to the previous treatment (e.g., if A was color red and B was green in a given treatment for a particular bird, then A



**Fig. 2.** Rate of food intake of a generalist (filled diamonds; i.e., a bird always choosing A and B over R in sequential choices) and of a specialist (open diamonds; i.e., a bird choosing A over R and R over B in sequential choices) as a function of the delay to food in option B. Delay to food in option A was 1 s in all treatments. Panel A presents predictions for an ideal animal that responds immediately to options. Panel B presents predictions that include observed latencies to respond in each treatment.

was green and B was red in the next treatment for that starling). This had the effect of inducing the animals to re-establish their preferences, avoiding a carry-over preference for A between treatments. The initial assignment of colors to options A, B, and R for each bird was randomized.

### 2.3.5. Dependent measures

The following variables were recorded: latency to peck the flashing side key (option latency), and proportion of choices for A over R, B over R, and A over B.

### 2.3.6. Statistical analyses

Latencies were transformed to natural logarithm and proportion of choices were square-root-arc sine transformed before statistical tests (Grafen and Hails, 2002; p. 179). Repeated measures analyses of variance (with five treatments) were done with latencies and proportion of choices. The value of  $\alpha$  was set at 0.05.

## 3. Results

### 3.1. Testing the sequential choice model

The SCM states that choices between simultaneously present options can be predicted from the latency to accept each option when found on its own. To test this prediction we recorded latencies observed during the training phase (when options were met sequentially and in isolation) and used them as predictors of the proportion of choices between pairs of options during the choice phase, when they were met simultaneously, in pairs. These predictions can be tested with various degrees of quantitative detail. First, to test if SCM correctly predicted the sign of preferences we compared the sign of the difference in central value of the latencies. Since the rate-maximizing models do not predict partial preferences, this test establishes if the location of the switch between strategies is correctly predicted.

To make predictions about the strength of partial preferences, we need to hypothesize the process by which the distributions of latencies are sampled. We come back to this later. In either case these tests depend on the descriptive statistics of the latencies during the training phase, when options were met one at a time and of preferences during the choice phase, when they were met in pairs. We present these in the next sections.

#### 3.1.1. Latencies to individual options during the training phase

Fig. 3 shows the latencies to options A, B, and R as a function of treatment during the last session of the training phase. As can be seen in the figure, the means of individual median latencies to A and R were more or less stable across treatments, while mean latency to B increased as the delay to food associated in

this option increased. A repeated measures ANOVA with latency as dependent variable yielded a significant effect of Treatment [ $F(4, 20) = 11.87, p < 0.001$ ]; Option, [ $F(2, 10) = 44.61, p < 0.001$ ] and treatment  $\times$  option interaction, [ $F(8, 40) = 13.78, p < 0.001$ ]. The main effects of treatment on latency were non significant for A or for R [ $F(4, 20) < 1$  and  $F(4, 20) = 1.73$ , respectively] but significant for B [ $F(4, 20) = 27.13, p < 0.001$ ]. Post hoc contrasts on latency to B across treatments ( $\alpha_C = 0.05/10 = 0.005$ ) showed no significant differences among treatments 1, 2 and 3, or between treatments 4 and 5 (all  $p$ -values  $> 0.01$ ), but latencies for B in treatments 1, 2, and 3 were significantly shorter than in treatments 4 and 5 (all  $p$ -values  $< 0.005$ ).

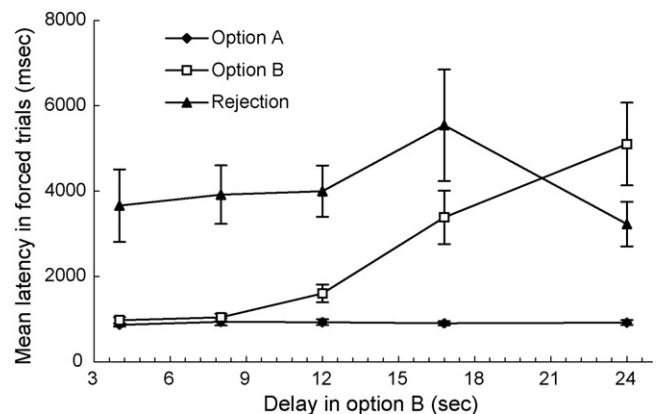
### 3.2. Preferences during the choice phase

#### 3.2.1. Simultaneous choices

Mean percentage of choices for option A over B was above 90% in all treatments. In spite of preferences being so extreme, an ANOVA of square-root-arc sine transformed preferences with treatment as a factor detected significant differences among treatments [ $F(4, 20) = 6.22, p = 0.002$ ]. Post hoc contrasts ( $\alpha_C = 0.005$ ) showed reliable differences between treatment 1, (mean proportion of choices for A over B  $\pm 1$  S.E.M.:  $0.94 \pm 0.02$ ) and treatments 4, ( $0.99 \pm 0.002$ ), and 5, ( $0.99 \pm 0.005$ ). All other comparisons were non-significant (all  $p$ -values  $> 0.005$ ).

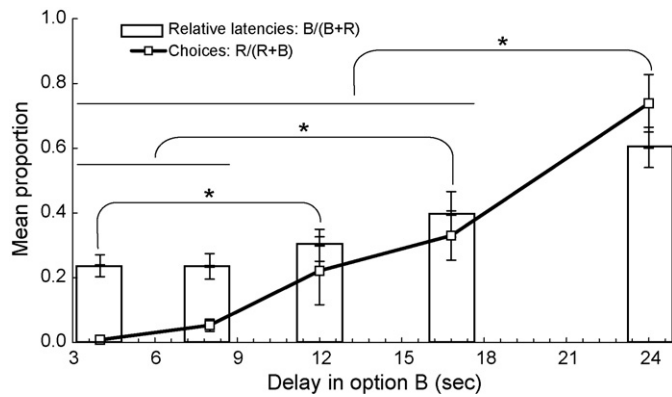
#### 3.2.2. Sequential choices

According to the rate maximization rationale the richer options should never be rejected. Accordingly, the proportion of choices of



**Fig. 3.** Latencies to options A, B, and R in forced trials of the last session of the training phase as a function of treatment. Error bars denote  $\pm 1$  S.E.M.





**Fig. 4.** Mean proportion of *B*–*R* relative latencies in forced trials and choices in sequential choice trials (i.e., preference for *R* over *B*) as a function of treatment. Error bars denote  $\pm 1$  S.E.M. Asterisks represent reliable differences in proportion of choices among treatments.

*A* over *R* was almost absolute and mostly unaffected by treatment (mean proportion of choice for *R* over *A* averaged across treatments  $\pm 1$  S.E.M.:  $0.005 \pm 0.003$ ).

In contrast, diet choice models do predict rejections of the leaner option under certain conditions (see Fig. 2). Fig. 4 shows the mean proportion of choices for *R* over *B* as a function of treatment. Rejection of *B* increased with increments in *B*'s delay. The square-root-arcsine transformation of choice proportions normalized residuals and reduced the difference in variances across treatments. The ANOVA of transformed proportions showed a significant effect of treatment [ $F(4, 20) = 34.72, p < 0.001$ ].

We can summarize the predictions regarding the sign of preference between options (namely the predominance of generalist vs. specialist strategies) for both the rate-maximizing and the sequential choice models, comparing Figs. 2–4. The classic diet choice model (Fig. 2A) predicted a generalist strategy (accepting both *A* and *B*) for treatments 1 and 2, neutrality for treatment 3, and a switch to the specialist strategy (namely rejection of option *B* in favor of *R*) for treatments 4 and 5, while the modified diet choice model (Fig. 2B) predicted a generalist strategy for treatments 1–4 and a switch to specialist only for treatment 5. For the SCM, Fig. 3 shows that mean latencies were only shorter for *R* than for *B* in treatment 5, hence this model predicts a switch to rejection of *B* for the same treatments as the modified diet choice model. Fig. 4 shows that *R* was preferred over *B* only for treatment 5, thus supporting the predictions of both the modified diet choice model and SCM.

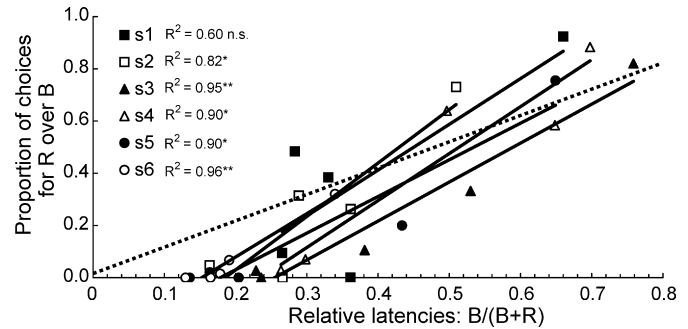
### 3.2.3. Quantitative test of SCM

In order to test if the SCM could predict the level of partial preferences, one needs to postulate how the distribution of latencies gives rise to choices (see Shapiro et al., 2008, Eq. (6)). In the present case, we instead use the relative value of latencies for *R* and *B* ( $\text{RelLat}_{R,B}$ ) in the last session of the training phase as a predictor of magnitude of preference in the choice phase, using the following equation:

$$\text{RelLat}_{R,B} = \frac{\text{latency for } B}{\text{latency for } B + \text{latency for } R} \quad (1)$$

Notice that longer latency for *B* means higher predicted choice for *R*. Fig. 5 shows the proportion of choices for *R* over *B* of each subject and treatment as a function of that subject's relative latency.

The figure shows similar slopes and intercepts for all subjects, with the amount of variance explained ranging from 60% to 96%. Although each regression is based in only 5 points, this led to significant regressions for 5 of the 6 subjects.



**Fig. 5.** Individual regressions of proportion of choices for *R* over *B* in each treatment against mean relative latency between these two options in forced trials [i.e., latency to *B*/([latency to *B* + latency to *R*)]]. The dashed line represents a straight line with slope = 1, and intercept = 0. n.s.: non significant; \* $p < 0.05$ ; \*\* $p < 0.01$ .

## 4. Discussion

Using the framework of a classical foraging problem we addressed two independent issues: to what extent rate maximization predicts choice, and what are the behavioral mechanisms mediating the process. Our experimental paradigm was based on the diet choice problem introduced by Charnov (1976). The idea is to consider a consumer that encounters more than one kind of prey, one type at a time. On each encounter, the consumer can either go after the present prey or skip it to return to a search mode, in which any prey type can be met. Charnov's model determines the conditions under which overall rate of gain is greater if the subject skips poor prey types, paying a cost of extra searching in exchange for spending more of its time involved with higher profitability prey types. As with most optimality models, parameterization to test predictions against behavior poses the problem of how much of the animal's self-imposed costs are introduced in making predictions. As we include details of observed behavior, the model loses some power of independent prediction but increases its chances of a good quantitative fit. In our case, we found that predictions based purely on programmed values had the right trend but suggested greater tendency to become a specialist than actually observed. However, when the self-imposed latencies to accept food items were included in the searching costs, the model was precise in its predictions for the switch between strategies. This was because the animals took longer times to peck at the rejection stimulus than to the poor rewarded stimulus, so that the cost of switching to a searching mode relative to profitability of the poorer option was greater than those of an ideal instantaneously responding animal. Another way to put it is that the ideal model overestimates realizable rates of intake by ignoring ever-present time costs.

This importance of self-imposed latency is the key to the mechanistic Sequential Choice Model. Corroborating the observations of Shapiro et al. (2008), we found that the stimuli associated with each expected outcome led to a systematically different latency to respond. We measured these latencies in a phase of the experiment when opportunities were met in isolation, and had to be taken to advance to the next trial, then used the resulting latencies to predict how the animal would choose when facing stimuli in pairs. In the choice phase of our experiment three stimuli, corresponding to two rewarded opportunities and one resetting option that initiated the search mode earlier but without reward were offered in pairs. We found that latencies during the forced-trial of the training sessions were accurate in predicting choices in the choice phase, when options were met in pairs, including the choice between the leaner rewarded option and the rejection key: only in the treatment in which latencies to the rejection key in forced trials were shorter than those to the leaner rewarded option did the birds prefer the rejection key in choice trials, thus acting as specialists.

Thus the sequential choice model, or SCM, provides a mechanism for rate-maximizing choices.

The mechanism that determines starlings' readiness, or latency, to pursue a given option in forced trials, requires itself being investigated, since any delay to respond implies lost foraging opportunity. It should be noted that subjects facing schedules of reinforcement such as ours learn to respond to arbitrary stimuli that, through training, become predictive signals of specific outcomes. In our case the distinctive outcomes were different delays to biologically significant events (i.e., food). The process by which originally neutral stimuli acquire value could be modeled as the acquisition of associative strength by any conditioned stimulus that is followed by an unconditioned one under certain contingencies. The standard process of classical conditioning, and in particular the Rescorla–Wagner model (Rescorla and Wagner, 1972) can be modified to yield the observed preferences if a suitable performance rule (namely some process for translating associative strength into responding is incorporated (Freidin and Kacelnik, unpublished, but see Freidin, 2007).

It is not surprising that models of a different nature converge to similar predictions: natural selection weeds out mechanisms of either learning or steady-state performance that do not approximate the behavior scientists identify using optimality models, if the models are sufficiently well tuned to the ecological circumstances in which the species lives and evolves. As Sara Shettleworth has shown in many of her studies, functional and mechanistic views of behavior go, and must go, hand in hand. We hope to have shown one instance of this desirable integration.

## Acknowledgements

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## Appendix A. The diet choice model

This appendix summarizes the classic diet choice rate maximization model (Charnov, 1976), explains suitable modifications introduced by Cassini and Kacelnik (1994) and explains their application to the present study.

Consider a forager that encounters prey on average every  $VT$  seconds of searching. Two prey types,  $A$  and  $B$ , are met with probabilities  $p_A$  and  $1 - p_A$ , respectively. If attacked, prey  $A$  delivers  $amt_A$  food units after  $delay_A$  seconds, while  $B$  yields  $amt_B$  after  $delay_B$  seconds. Arbitrarily we define prey type  $A$  as having a greater ratio  $amt/delay$ .

Following Charnov (1976) we start by considering the returns of units of food per unit of time that would obtain ideal predators that consumed every prey encountered immediately (generalist). The ideal generalist's overall rate of gain is given by the following equation:

$$\text{generalist rate} = \frac{(p_A \times amt_A) + [(1 - p_A)amt_B]}{(p_A \times delay_A) + [(1 - p_A)delay_B] + VT} \quad (A.1)$$

In contrast, a specialist that rejected all  $B$  immediately would experience the following rate of returns:

$$\text{specialist rate} = \frac{p_A \times amt_A}{(p_A \times delay_A) + VT} \quad (A.2)$$

These two basic equations can be used to determine the treatments under which either of the two rates would be higher. In the

present experiment  $amt_A = amt_B$ ,  $p_A = p_B = 0.5$ ,  $VT = 5.5$  s,  $delay_A = 1$  s and  $delay_B$  varied between treatments. Fig. 2A shows the expected rates of the two strategies according to Eqs. (A.1) and (A.2) for all our treatments.

As Cassini and Kacelnik (1994) have pointed out, however, these basic equations are unrealistic because they assume that the specialist pays no time cost for rejecting a poor option to restart searching. In an experiment with guinea pigs (*Cavia aperea*), they found that predictions were in fact affected by including recognition times, and the behavior of their subjects was closer to rate maximization when this unavoidable constraint was included. Similarly, Shapiro et al. (2008) showed that choices between simultaneously present alternatives could be predicted more accurately when the latency to respond actually shown by the animals was included in the computations of rate. In our experimental situation, there are three times systematically different latencies between the onset of each opportunity for choice ( $A$ ,  $B$  or  $R$ ) and the subject's response ( $Lat_A$ ,  $Lat_B$  and  $Lat_R$ , respectively). The effect of this is to add different constants to  $delay_A$  and  $delay_B$  and to include the latency to  $R$  in the time cost whenever the subject rejects  $B$ . Defining  $dObs_A = Lat_A + delay_A$  and  $dObs_B = Lat_B + delay_B$ , Eqs. (A.1) and (A.2) transform into the following equation:

modified generalist rate

$$= \frac{(p_A \times amt_A) + [(1 - p_A)amt_B]}{(p_A \times dObs_A) + [(1 - p_A)dObs_B] + VT} \quad (A.3)$$

In contrast, a specialist that rejected all  $B$  immediately would obtain the following equation:

modified specialist rate

$$= \frac{p_A \times amt_A}{(p_A \times dObs_A) + (1 - p_A)Lat_R + VT} \quad (A.4)$$

Fig. 2B shows these two rates computed for our experimental treatments. The observed delays we taken to be the cross-subject mean values for each treatment. The rates are less regular than those in Fig. 2A because they include empirical values.

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