

TESTING DYNAMIC RULES OF ANIMAL COGNITIVE PROCESSING WITH LONGITUDINAL DISTRIBUTION DATA

Fushing Hsieh^{1,3}, Shwu-Bin Horng², Hui-Ying Lin³ and Yen-Chiu Lan³

¹*University of California at Davis*, ²*National Taiwan University*
and ³*Academia Sinica*

Abstract: Identifying the cognitive capacity used by an animal to resolve its foraging task when facing ever-changing environmental conditions is a recent, central issue in behavioral ecology and cognitive science. Statistical confirmation of potential capacity through analysis of individual behavioral processes becomes an important research topic. New longitudinal data arise as a sequence of global quality distributions, representing sparsely observed environmental dynamics. Such dynamics result from an individual animal's decision-making process as it explores a patch that consists of a fixed amount of hosts. Three dynamic rules having distinct degrees of cognitive capacities are analyzed under a time-varying Markov structure. From the perspective of goodness-of-fit, two test statistics are proposed for capturing different aspects of dynamic changes in the environment. It is found that the test that best embraces the concept of distribution via the receiver operating characteristic (ROC) curve performs quite well.

Key words and phrases: Egg-distribution data, goodness-of-fit test, martingale central limit theory, maximum likelihood approach, receiver operating characteristic (ROC) curve.

1. Introduction

Recent research in interdisciplinary cognitive ecology, emerging from cognitive science and behavioral ecology (Real (1993), Dukas (1998) and Shettleworth (1998)), is based on the view that an animal's dynamic behavioral process consists of two interacting mechanisms: information processing and decision-making. Statistical inference regarding these two mechanisms, based on observed animal behavioral processes, has become an important. The information processing is concerned with what kind of information is collected by an animal along its searching trajectory in an experimental or natural environment, while decision-making is aimed at how a specific decision is made. Biologically, these two mechanisms are two inseparable aspects of the animal behavior as a whole-mate choice, habitat selection, host or diet selection in the field or in the experimental

study (Luttbeg (1996) and Wiegmann, Real, Capone and Ellner (1996)) and are central issues in behavioral ecology (Krebs and Kacelnik (1991) and Real (1993)).

The two underlying mechanisms are further interpreted as follows: information processing collects and evaluates the “potential” of experienced resource objects pertaining to a designated biological purpose; decision making is to accept or reject the currently encountered resource item based on a segment of potential information stored in the animal’s brain. This interpretation is advocated in Sherman, Reeve and Pfennig (1997), and applied to mate choice in Getty (1995, 1996). Our discussion in the present paper is based on this interpretation. We further attempt to quantify the concept of “potential”. While any quantification might only reflect a researcher’s subjective biological reasoning, it leads to goodness-of-fit testing rather than estimation. We focus on the development of goodness-of-fit testing as a way to confirm individual animal cognitive capacity. The corresponding capability on the population level is meant to be a summary of individual-based analysis.

Considers quantitative “potential” Horng (1997) in the female cowpea weevil, *Callosobruchus maculatus*. For an i -egg azuki bean, let S_i be the probability of success of one of i eggs laid on the bean. Here the success of an egg is that a young hatched from this egg goes through several developmental stages within the bean and merges as an adult beetle. With this definition of success, the fitness of a bean is taken to be the expected total number of successes of the its eggs. The potential of an i egg bean as a host to a female cowpea weevil is defined as the following increment in fitness:

$$g_i = (i + 1)S_{i+1} - iS_i.$$

That is, g_i is the gain of fitness value from one more egg on an i -egg bean. It is speculated that a female beetle would accept an i egg to lay one more egg with probability

$$P_i = \frac{g_i}{g_0} = \frac{[(i + 1)S_{i+1} - iS_i]}{S_1}.$$

In a previous experiment, fitness values were empirically observed, see Horng (1997), and modeled through $S_i = \alpha(i)^{-\beta}$, with $\alpha = S_1$, and β denoting the larval competition coefficient. Numerically, α and β were estimated by 0.96 and 0.496, respectively. Thus a female beetle having the capacity of evaluating the potential of a host bean would accept an i egg bean with probability $P_i = (i + 1)(i + 1)^{-0.496} - i(i)^{-0.496}$ $i = 1, 2, 3 \dots$, with $P_0 = 1$.

We compare three dynamic rules embedded with different degrees of cognitive capabilities upon encountering an i egg bean with probability P_i .

1. Random rule (R_A): always accept.
2. Absolute rule (A_B): accept with probability P_i .

3. Relative rule (R_E): if the previously encountered bean does not have higher potential, accept this i egg with probability P_i ; otherwise, reject.

Apparently these three dynamic rules have increasing cognitive capacity in the order R_A , A_B , R_E . Heuristically, R_A uses neither information processing nor decision-making capacities. The rule A_B is limited to information of the currently encountered bean. In contrast, R_E uses the information of the currently encountered bean and compares it with that of the previous. The rule does require memory capacity.

At any point of temporal order of oviposition, a distribution of i egg beans, $i = 0, 1, 2, \dots$ describing the composition of host quality within an environment consisting of a fixed number of host beans is called an egg-distribution. Equipped with a random locomotion algorithm, all three rules R_A , A_B and R_E induce a specific time-varying Markov transition probability on egg-distributions with the total number of oviposition as the time scale.

Due to a fixed observation schedule, only longitudinal data of egg-distributions is available for individual females. Thus, based on each longitudinal profile, we need to impute all missing segments to compute its corresponding probability. The likelihood of a dynamic rule contributed by a single female is equal to the sum of probabilities ranging over all possible trajectories subject to the given individual longitudinal profile. Algorithmic computational complexity in such a likelihood reconstruction is similar to that found in applications of the hidden Markov model.

Comparing the three likelihood values, we can choose the highest among the three dynamic rules. Such a choice might not be biologically realistic. Hence an effective goodness-of-fit testing is a necessity. However the egg-distribution is discrete. Summarizing such data in a scalar is an option we use to carry out our statistical inferences. Since only one aspect of the distribution data is brought out by a particular algorithm, and leaves behind many other aspects. Two summarizations are considered here: error number, previously used in Horng (1997); area under the receiver operating characteristic (ROC) curve, which has been widely used in signal detection theory (Hsieh and Turnbull (1996)).

With a chosen summarization algorithm, martingale differences between observed values and conditional expectations under a dynamic rule are natural ingredients for the goodness-of-fit statistic. Two martingale testing statistics are derived, and inference is based on the Martingale Central Limit Theorem (Hall and Heyde (1980)).

As the main goal is to confirm individual cognitive capacity embedded in observed behavioral process, we mention our biological stand here. The diversity, of animal behavior is considerable. The variation is itself of great importance

when evolution via natural selection is involved. We refrain from making species-specific conclusions on behavioral traits. In part, this is due to the issue of uneven information content contributed by different individuals. Technical difficulties are relegated to the Discussion section. At this stage, how to properly pool individual data for testing hypotheses at the population level remains an open problem.

The organization of this paper is as follows. In Section 2, experimental and observational settings are explicitly described. In Section 3 likelihood functions, as well as conditional expectations under the three dynamic rules, are derived. Some technical details are given in the Appendix. Two martingale testing statistics are derived and shown to be approximately normal in Section 4. Two sets of data from experiments reported in Horng (1997) are analyzed in Section 5. In Section 6, some related issues are discussed.

2. Egg-Distribution Data and Its Conditional Expectation under Dynamic Rules

The experimental setting is a Petri dish containing N azuki beans on which the female beetle carries out its cognitive processing. Beans are assumed to be indistinguishable from outward appearance, and uniform in quality. At any point of time, the quality level of a bean is indicated by its egg-load, $0, 1, 2 \dots$, in decreasing favor. As in mate choice, a male have mated once with a female animal is assumed to have a lower quality than one which has not mated, other qualities being equal (Gibson and Langen (1996)), and similar assumptions have seen made in habitat selection studies (Manly, McDonald and Thomas (1993) and Sutherland (1996)), and in diet selection (Stephens and Krebs (1986) and Godfray (1994)).

Let x be the total number of egg laid by a female, and $a_i(x)$ be the observed fraction of i -egg beans. Hence, at the time x , the egg-distribution is the vector $a(x) = (a_0(x), a_1(x), a_2(x), \dots)$ with $\sum_{i=0}^k a_i(x) = 1$, k some default number. An individual longitudinal profile is denoted by $(a(x_1), \dots, a(x_n),)$ with x_i being the egg number produced by the female up to the i -th observation, with n is the total number of observations.

With complete random locomotion and a Markov structure, conditional expectations of the egg-distribution, $E[a(x+k)|a(x), H]$, of $a(x+k)$ given $a(x)$, under a dynamic rule $H \in \{R_A, A_B, R_E\}$, are given as follows.

(I) Under R_A ,

$$E[a_0(x+1)|a(x), R_A] = a_0(x) - \frac{a_0(x)}{N}$$

$$E[a_j(x+1)|a(x), R_A] = a_j(x) - \frac{a_j(x)}{N} + \frac{a_{j-1}(x)}{N}, \quad \text{for } j = 1, 2, \dots,$$

(II) Under A_B ,

$$E[a_0(x+1)|a(x), A_B] = a_0(x) - \frac{a_0(x)P_0}{N \cdot P_{A_B}[a(x)]}$$

$$E[a_j(x+1)|a(x), A_B] = a_j(x) - \frac{a_j(x)P_j}{N \cdot P_{A_B}[a(x)]} + \frac{a_{j-1}(x) \cdot P_{j-1}}{N \cdot P_{A_B}[a(x)]}, \text{ for } j = 1, 2, \dots,$$

where $P_{A_B}[a(x)]$ is the acceptance probability per encounter, $P_{A_B}[a(x)] = \sum_{i=0}^k a_i(x)P_i$. Thus the conditional probability given $a(x)$, under A_B , that a female beetle encounters an i -egg bean and decides to accept it as a host for oviposition is

$$\Pr(\delta^{A_B}(x+1) = i | a(x), A_B) = \frac{a_i(x) \cdot P_i}{P_{A_B}[a(x)]}.$$

This is proved in the Appendix.

(III) Under R_E , the probability that a female beetle encounters an i -egg and decides to accept it is

$$\Pr(\delta^{R_E}(x+1) = i | a(x), R_E) = \frac{\frac{1}{N-1} \left(N \sum_{j=i}^k a_j(x) - 1 \right) \cdot a_i(x) \cdot P_i}{P_{R_E}[a(x)]},$$

where the acceptance probability per encounter is

$$P_{R_E}[a(x)] = \frac{1}{N-1} \sum_{i=0}^k \left(N \sum_{j=i}^k a_j(x) - 1 \right) \cdot a_i(x) \cdot P_i.$$

Therefore,

$$E[a_0(x+1)|a(x), R_E] = a_0(x) - \frac{a_0(x)P_0}{P_{R_E}[a(x)]},$$

$$E[a_j(x+1)|a(x), R_E] = a_j(x) - \frac{\frac{1}{N-1} \left(N \sum_{i=j}^k a_i(x) - 1 \right) \cdot a_j(x) \cdot P_j}{P_{R_E}[a(x)]}$$

$$+ \frac{\frac{1}{N-1} \left(\sum_{i=j-1}^k a_i(x) - 1 \right) \cdot a_{j-1}(x) \cdot P_{j-1}}{P_{R_E}[a(x)]}, \text{ for } j = 1, 2, \dots$$

See the Appendix.

Note that $\delta^{RE}(x+1)$ and $\delta^{AB}(x+1)$ are multinomial random variables with probabilities changing with the cumulative egg number, x , as well as with the previous egg-distribution. In this sense, both $\{\delta^{RE}(x)\}$ and $\{\delta^{AB}(x)\}$ are inhomogeneous discrete-time Markov chains.

Let $\{a^*(x+1), a^*(x+2), \dots, a^*(x+k-1)\}$ be an unobserved segment of egg-distribution trajectory leading from observed $a(x)$ to $a(x+k)$. Then

$$\begin{aligned} & \Pr(a^*(x+1), \dots, a^*(x+k-1), a^*(x+k) | a(x), H) \\ &= \left\{ \prod_{j=1}^{k-1} \Pr(a^*(x+j) | a^*(x+j-1), H) \right\} \Pr(a^*(x+k) | a^*(x+k-1), H). \end{aligned}$$

Further, let $S[a(x) \rightarrow a(x+k)]$ be the set of all possible missing segments leading from $a(x)$ to $a(x+k)$. Then

$$\begin{aligned} & \Pr(a(x+k) | a(x), H) \\ &= \sum_{S[a(x) \rightarrow a(x+k)]} \Pr(a^*(x+1), \dots, a^*(x+k-1), a^*(x+k) | a(x), H). \end{aligned}$$

Finally, the likelihood function of $H \in \{R_A, A_B, R_E\}$ given the set of resource quality dispersion $(a(x_1), \dots, a(x_n))$ is $L(H) = \prod_{j=0}^{n-1} \Pr(a(x_{j+1}) | a(x_j), H)$.

The maximum likelihood choice among $H \in \{R_A, A_B, R_E\}$ can be obtained by comparing among three values, $L(R_A)$, $L(A_B)$ and $L(R_E)$. Still this choice could be far from a realistic underlying generating mechanism for the observed longitudinal profile $(a(x_1), \dots, a(x_n))$. We turn to goodness-of-fit testing.

3. Martingale Testing Statistics

Given $E[a(x+k) | a(x), H]$, $H \in \{R_A, A_B, R_E\}$, a component of the vector of differences between the observed and expected egg-distributions is $a(x+k) - E[a(x+k) | a(x), H]$. Under the Markov structure, this component is a martingale difference, assuming that H is the true dynamic rule. Its vector form prevents its immediate use in goodness-of-fit testing. We consider two real-valued characterizations of an egg-distribution: one is an error number, and the other is the area under a receiver operating characteristic (ROC) curve. For the (biological) error number, superparasitism (laying eggs into parasitized host, or accepting a 1-egg bean) by parasitoids is regarded as a mistake. This consideration was also used in Horng (1997). The latter number is a popular characteristic for comparing two distributions in signal detection, and is closely related to Mann-Whitney statistics. See Hsieh and Turnbull (1996) for more details and related asymptotic developments. It has also been applied to mate choice behavior, see Getty (1995, 1996). Based on the two martingale differences, testing statistics are derived.

First, based on the idea of optimal foraging theory, the error number pertaining to an egg-distribution, $a(x)$, is taken to be the minimum number of actions to remove one egg at a time from one resource item to another in order to achieve a uniform egg-distribution (e.g., Messina and Mitchell (1989) and Horng (1997)). For instance, there are two mistakes that give rise to an egg-distribution $20 \cdot a(10) = (12, 6, 2, 0, 0, \dots, 0)$ with $N = 20$: by removing one egg from both 2-egg beans in $a(10)$ to two 0-egg-beans, we can arrive at a uniform egg-distribution $(10, 10, 0, \dots, 0)$.

Let $\mathfrak{S}[a(x)]$ be the error number pertaining to $a(x)$, and denote the increment of error number from $a(x_{i-1})$ to $a(x_i)$ as $e_i(x_i) = \mathfrak{S}[a(x_i)] - \mathfrak{S}[a(x_{i-1})]$. Then the martingale difference related to $e_i(x_i)$ under the dynamic rule H is

$$m_{1i}^H = e_i(x_i) - E[e_i(x_i)|a(x_{i-1}), H]$$

and its predictable variation is $V_{1i}^H = \text{Var}[m_{1i}^H|a(x_{i-1}), H]$. By applying the Martingale Central Limit Theorem, see Hall and Heyde (1980), the statistic $M_1^H = \sum_{i=1}^k m_{1i}^H / \sqrt{\sum_{i=1}^k V_{1i}^H}$ is approximately distributed as $N(0, 1)$ under the hypothesis that H is the true dynamic rule.

The second characterization is the area under a receiver operating characteristic (ROC) curve constructed by comparing the observed egg-distribution to its corresponding conditional expectation.

The idea is that, under the hypothesis that H is the true dynamic rule used by the female, the two distributions pertaining to the observed egg-distribution and its conditional expected egg-distribution should be close to each other. Indeed the ROC curve is simply the P-P plot of these two distributions on $\{0, 1, 2, 3, \dots, k\}$, that is, the curve

$$\left(\sum_{j=0}^{\ell} E[a_j(x_i)|a(x_{i-1}), H], \sum_{j=0}^{\ell} a_j(x_i) \right), \ell = 0, \dots, k.$$

Then the martingale difference involving $a(x_i)$ is $m_{2i}^H =$ the area under the above ROC curve $-1/2$. In fact this area is a linear combination of components in the vector of martingale differences $a(x+k) - E[a(x+k)|a(x), H]$. Correspondingly its predictable variation can be calculated, and is denoted by $V_{2i}^H = \text{Var}[m_{2i}^H|a(x_{i-1}), H]$. Again, by applying the Martingale Central Limit Theorem, the testing statistic $M_2^H = \sum_{i=1}^k m_{2i}^H / \sqrt{\sum_{i=1}^k V_{2i}^H}$ is approximately distributed as $N(0, 1)$ under the true dynamic rule H .

As far as the technical validity of the martingale central limit theory is concerned, simulation studies conducted under different dynamic rules show sat-

isfactory normal approximations in terms of Q-Q plots, see Lin (1998) for more detail numerical computations.

4. Experimental Settings and Results of Data Analyses

Before describing the experimental setting from which the egg-distribution data is observed, and our data analyses, a brief description of the cowpea weevil, *Callosobruchus maculatus*, is helpful for understanding the female's behavior (e.g., Wilson (1988), Messina and Mitchell (1989), Mitchell (1990), Horng (1997) and Horng, Lin, Wu and Godfray (1999)). A female beetle is seen uniformly distributing her eggs on the azuki beans available to her. The functional reason is to reduce the extent of competition that her young could possibly face. Her young, after hatching, will break through the surface and eat into the bean. They remain inside the bean and grow until emerging as adults. A young grown-up facing less competition in a bean has a higher probability of success. Thus the capacity of uniformly distributing her eggs is considered as an adaptation to improve offspring survival, (Mitchell (1975, 1990)), and is also speculated as an optimization foraging mechanism (Visser (1995)).

Our longitudinal data were collected from two experiments. In the first, nine 1-day-old mated females are placed individually into 5-cm petri dishes, each containing 100 ($= N$) azuki beans as resource items. In the second, each of ten 1-day-old females is given 20($= N$) azuki beans. All petri dishes are placed inside an incubator with no light, under constant temperature and humidity. On a fixed schedule, in every 24 hour period for 7 ($= m$) days, petri dishes are out of the incubator for a short time and egg-dispersion is recorded.

Table 1. Likelihood of the three dynamic rules.

Beetle #	Bean number = 20			Beetle #	Bean number = 100		
	Random	Absolute	Relative		Random	Absolute	Relative
1	3.50E-12	3.32E-10	8.45E-04	1	3.70E-12	8.50E-06	8.45E-04
2	4.73E-12	2.50E-08	2.34E-06	2	6.20E-12	1.30E-06	8.37E-06
3	5.45E-16	1.85E-10	6.33E-07	3	1.30E-04	1.00E-02	8.60E-02
4	1.99E-12	2.63E-10	1.04E-06	4	3.50E-13	1.80E-06	8.90E-04
5	1.85E-16	3.53E-12	1.06E-09	5	2.00E-09	9.40E-07	2.45E-08
6	2.91E-13	6.86E-10	1.60E-10	6	9.30E-12	3.70E-08	6.35E-10
7	7.00E-14	8.48E-10	6.21E-06	7	1.30E-11	1.20E-06	4.75E-06
8	2.84E-11	6.58E-08	3.32E-05	8	5.20E-09	2.30E-06	0
9	9.17E-13	3.78E-09	1.19E-06	9	8.40E-10	1.30E-06	5.18E-06
10	3.29E-15	2.22E-11	5.26E-11				

Based on individual egg-distribution profiles, our longitudinal data analyses are reported as follows. In Table 1, the individual likelihood value of each rule is reported for both experiments. From the experiment with 20 beans, except for

the #6 female, the other female beetles have the relative rule R_E as the MLE choice. The #10 female is not decisive. In contrast, in the experiment with 100 beans, the #5, #6 and #8 females' MLE choice is the absolute rule A_B , while the other six have the relative rule R_E as the ML choice. An experimental factor is speculated for this discordance in the last section. The random rule is not likely the dynamic rule used by any female bean weevil.

In Table 2, the test statistics M_1 and M_2 are calculated for the experiment with 20 beans; Table 3 does the same for 100 beans. From Table 2, by setting the nominal level to 0.05, M_1 and M_2 indicate that all ten females reject the random rule R_A . The absolute rule A_B is rejected by all beetles based on M_1 values, but not rejected by M_2 on the #2, #6, #9, and #10 female beetles. The relative rule R_E is rejected by M_1 on the #3 female, and by M_2 on two females (#6 and #10).

We conclude that, except for the #6 and #10 females, the relative rule best fits the strategy used by female cowpea weevils. The testing statistic M_1 is not reliable to use for the particular purpose considered here, since it produces inconsistent results.

In Table 3, the results for M_2 are in complete agreement with that in Table 1, with the #5, #6 and #8 beetles rejecting the relative rule and in favor of the absolute rule. The absolute rule is not rejected by M_1 for #3, #5, #8, and #9 females. This does not quite match with that of in Table 1. The disagreement further indicates that the error number used in M_1 might not be a good choice for summarizing egg-distributions.

In summary, M_2 provides a more reliable goodness-of-fit testing result than M_1 . However, research effort could be more conclusive about individual female cognitive capacity.

Table 2. M_1 and M_2 martingale testing statistics for an experiment with 20 beans.

Beetle #	Random		Absolute		Relative	
	M_1	M_2	M_1	M_2	M_1	M_2
1	-3.28	-2.10	-1.85	-1.60	-0.17	-0.049
2	-3.72	-2.12	-2.39	-1.28	-0.55	0.66
3	-4.16	-2.44	-3.16	-1.76	-1.74	-0.45
4	4.19	-2.59	-3.16	-1.87	-1.22	0.13
5	-3.68	-2.58	-2.63	-1.87	-1.24	0.12
6	-3.76	-1.72	-2.30	-0.85	-0.38	1.70
7	-4.10	-1.57	-2.75	-1.76	-1.40	0.22
8	-3.88	-2.34	-2.38	-1.73	-0.53	-0.12
9	-3.43	-2.25	-2.04	-1.57	-0.60	-0.42
10	-3.41	-1.84	-2.70	-0.92	-0.37	1.64

Table 3. M_1 and M_2 martingale testing statistics for an experiment with 100 beans.

Beetle #	Random		Absolute		Relative	
	M_1	M_2	M_1	M_2	M_1	M_2
1	-5.54	-4.24	-2.80	-2.23	-0.86	-0.32
2	-4.89	-3.96	-1.93	-1.68	0.31	0.77
3	-2.91	-2.60	-1.67	-1.50	-0.27	-0.22
4	-5.88	-4.71	-3.14	-2.78	-1.31	-0.12
5	-3.16	-2.79	-0.06	-0.27	2.99	3.31
6	-4.74	-3.38	-1.94	-1.02	0.24	1.72
7	-4.79	-3.89	-1.90	-1.60	0.32	0.69
8	-3.36	-2.51	-1.11	-0.47	-1.29	2.30
9	-3.63	-3.66	-0.72	-1.51	1.74	0.86

5. Discussion

Our tests should have a wide spectrum of applicability in animal cognitive research. Advances in understanding genetic mechanisms responsible for cognitive capacity can be most likely achieved by comparing genetic make-up among different strains of varying capacities. Our techniques have potential for such kind of individual selection in the process of strain construction.

An important issue is how to effectively extract pertinent information from an egg-distribution to confirm a specific cognitive capacity. Only when such information is available, can an efficient test be derived for the biological goal. We believe the information extracted via the ROC curve to be a good choice. For one, its linearity renders simpler conditions for the Martingale Central Limit Theorem to hold. Hence the finite sample approximate normality of M_2 is expected to be reasonable.

We emphasize that our goodness-of-fit testing is performed on an individual basis, rather than pooling across individuals, since it is unrealistic to assume homogeneous cognitive performance across any population. From an evolutionary perspective, the intra-population variability is the basis for evolution via natural selection (see Lomnicki (1988)). From a theory of life history perspective, beetles might have quite heterogeneous energy and protein reserve at maturity. These varying resources could profoundly affect the cognitive processing undertaken by a female beetle acting as a “decision maker” (see Krebs and Kacelnik (1991)). From an information perspective, it is necessary to differentiate the amount of information contributed by each individual’s egg-distribution profile. Heuristically, the amount of information might be measured by the total predictable variation of the martingale test statistics. The pertinent inferences on a population level must be derived in a form of weighted average. At this stage, a rigorous treatment on this issue is not yet been carried out.

Though estimation problems are not considered here, our martingale setups can be used as to construct estimating equations for the P_i . Also, our model setting can be further relaxed to allow a wider spectrum of applicability of our techniques. For example, resource items like prey or diet can be removed from the foraging region, instead of being depleted. Then the time-varying characteristics pertaining to quality distribution and the probability of encountering the remaining items must be incorporated into a model for evaluations of animal cognitive performance.

Finally we discuss the slight discordance of results from the 20- and 100-bean experiments on 5-cm Petri dishes as exhibited in Tables 1, 2 and 3. There is a geometric difference in the display of host beans on the Petri dishes: 20 beans contained in 5-cm petri dish forms a single layer on the dish floor, while 100 beans form two layers. This double layer structure ensures that a female beetle in 100-bean setting requires maleessain to explore the bottom layer of beans. Hence the encountering probability among the 100 beans is inhomogeneous, and renders less uniform egg-distribution.

To go further, a separate experiment was conducted with 100 beans placed in a 9-cm, instead of a 5-cm, petri dish. Here 100 beans form a single layer on the bottom floor of the dish. As reported in Table 4, the data analysis based on longitudinal egg-distribution profiles from the new setting shows good agreement with that of the 20-bean experiment. We conclude that most of female cowpea weevils not only collect information about the currently encountered bean, but also about the previous one. The decision-making mechanism must involve performing comparisons of current with previous information.

Also it is of importance that information collected by an animal might be sensitive to the geometric display of resource objects in an experimental or natural environment upon which animal forages.

Table 4. Likelihood of the three dynamic rules when the female was provided with 100 azuki beans in a large petri dish.

# of female	Random	Absolute	Relative
#1	2.17E-29	3.36E-16	1.48E-11
#2	4.25E-35	3.89E-20	5.83E-15
#3	3.32E-29	2.64E-16	1.38E-11
#4	3.31E-31	1.73E-16	4.24E-12
#5	5.94E-17	2.71E-08	6.68E-06
#6	9.10E-26	3.03E-13	1.93E-09
#7	1.46E-27	4.23E-14	3.82E-09
#8	1.00E-30	3.90E-17	4.34E-12
#9	1.48E-14	5.40E-08	9.85E-07
#10	9.41E-25	8.73E-13	1.88E-09

Appendix

In this Appendix, we derive the probability of laying an egg on a i -egg bean given the egg-distribution $a(x)$ and the dynamic rule A_B or R_E . Here the relative rule R_E is assumed to involve a without-replacement sampling mechanism within the decision-making comparison. That is, an immediate revisit of a bean, which has just been visited, is not allowed. Such a constraint is not used between decisions partly due to the missing trajectory, and partly for computation simplicity. Indeed this constraint is a matter of choice. Likewise, similar formula can be derived by using random sampling with replacement within the decision-making comparison.

(I) For A_B :

$$\begin{aligned} \Pr(\delta^{A_B}(x+1) = i | a(x), A_B) &= a_i(x)P_i + \left\{ \sum_{j=0}^k a_j(x)(1-P_j) \right\} a_i(x)P_i + \left\{ \sum_{j=0}^k a_j(x)(1-P_j) \right\}^2 a_i(x)P_i + \cdots \\ &= \frac{a_i(x) \cdot P_i}{1 - \sum_{j=0}^k a_j(x) \cdot (1 - P_j)} = \frac{a_i(x) \cdot p_i}{P_{A_B}[a(x)]}. \end{aligned}$$

(II) For R_E :

$$\begin{aligned} \Pr(\delta^{R_E}(x+1) = i | a(x), R_E) &= \frac{1}{N-1} \left(N \sum_{j=i}^k a_j(x) - 1 \right) a_i(x) P_i \\ &+ \left(\frac{1}{N-1} \right)^2 \left\{ \sum_{j=0}^k a_\ell(x) - 1 \right\} a_j(x) (1 - P_j) + \sum_{j=0}^k \left(N \sum_{\ell=0}^{j-1} a_\ell(x) - 1 \right) a_j(x) \Big\} \\ &\times \left(\left(N \sum_{j=i}^k a_j(x) - 1 \right) a_i(x) P_i \right) \\ &+ \left(\frac{1}{N-1} \right)^3 \left\{ \sum_{j=0}^k a_\ell(x) - 1 \right\} a_j(x) (1 - P_j) + \sum_{j=0}^k \left(N \sum_{\ell=0}^{j-1} a_\ell(x) - 1 \right) a_j(x) \Big\}^2 \\ &\times \left(\left(N \sum_{j=i}^k a_j(x) - 1 \right) a_i(x) P_i \right) + \cdots \end{aligned}$$

$$\begin{aligned}
& \frac{1}{N-1} \left(N \sum_{j=i}^k a_j(x) - 1 \right) a_i(x) P_i \\
= & \frac{1}{N-1} \left(N \sum_{j=i}^k a_j(x) - 1 \right) a_i(x) P_i \\
& 1 - \left\{ \frac{1}{N-1} \sum_{j=0}^k \left(N \sum_{\ell=j}^k a_\ell(x) - 1 \right) a_j(x) (1 - P_j) + \frac{1}{N-1} \sum_{j=0}^k \left(N \sum_{\ell=0}^{j-1} a_\ell(x) - 1 \right) a_j(x) \right\} \\
& \left(N \sum_{j=i}^k a_j(x) - 1 \right) a_i(x) P_i \\
= & \frac{\sum_{j=0}^k \left(N \sum_{\ell=j}^k a_\ell(x) - 1 \right) a_j(x) P_j}{\frac{1}{N-1} \left(N \sum_{j=i}^k a_j(x) - 1 \right) a_i(x) P_i} \\
= & \frac{1}{P_{RE}[a(x)]}.
\end{aligned}$$

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Department of Statistics, University of California, Davis CA95616, U.S.A.

Institute of Statistical Science, Academia Sinica, Taipei, Taiwan.

E-mail: fushing@wald.ucdavis.edu

Department of Entomology, National Taiwan University, Taipei, Taiwan.

E-mail: sbhorng@ccms.ntu.edu.tw

Institute of Statistical Science, Academia Sinica, Taipei, Taiwan.

E-mail: huiying@math.ntu.edu.tw

Institute of Statistical Science, Academia Sinica, Taipei, Taiwan.

E-mail: yenchiu_lan@hotmail.com

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