FUNCTIONAL RESPONSE AND THE EFFECT OF A BAYESIAN PREDATOR ON PREY DISTRIBUTION

By Richard F. Green

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Department of Statistics
University of California
Riverside, California 92521

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Present address: Department of Mathematical Sciences,
University of Minnesota, Duluth, Duluth, Minnesota 55812

INTRODUCTION

Many early models of predator-prey systems* are mathematically unstable (Nicholson and Bailey 1935, Holling 1959, see Hassell and May 1973, Hassell 1978). However, the natural systems modelled, while showing population fluctuations, are not unstable in the sense that the interactions cause one species to go extinct.

An important assumption of some of the unstable models is that as the number of prey increases the number of prey taken per predator does not increase as fast. This results in what Holling (1959) calls a Type II functional response. A number of laboratory experiments show a Type II functional response but as Hassell et al. (1977) point out these results may be artifacts of the experimental design. In the experiments the predators search for large, palatable prey in a small, closed, homogeneous environment. Hassell et al. (1977) show that when the environment is more complicated and the prey is less obvious Type III functional responses are often seen. This is important because a Type III functional response may contribute to the stability of the system. This sigmoid functional response may be due to the fact that more energy is spent foraging when prey density is higher. At low prey density a predator saves his energy or spends it on activities other than foraging.

Models that assume random search for prey in a homogeneous environment may be simple, but they are also unstable. In fact, the environment is usually not homogeneous and search is probably not often random. Luck et al. (1979) have considered the consequences of predators foraging

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*Throughout this paper I will refer to predator-prey systems, even though many of the models are intended for parasitoid-host systems.

nonrandomly in a patchy environment. They consider various rules the predator could use to decide when to leave a patch. If the predator leaves a patch when it does not find a prey within some fixed time, or leaves after it has gone some other fixed time without finding any more prey, then a Type III functional response may be seen. Luck et al. (1979) think that one reason Type III functional responses were not seen in earlier experiments is that predator emigration was not permitted in those experiments.

The strategies that should be used by predators feeding in discrete patches have been considered by Charnov (1976). His "marginal value theorem" gives a rule that an optimal forager should use to decide when to leave a patch. Charnov's model is deterministic and, while he says his results may be extended to the stochastic case, Oaten (1977) has pointed out that Charnov's predator would have no way of knowing when to leave a patch in the stochastic case. Hassell and May (1974) and Murdoch and Oaten (1975) consider predators that use the rule: leave a patch if no prey are found within a fixed time interval. Such a rule, sometimes referred to as a "giving-up time" rule, is not optimal but it is at least possible to use. It does not require an omniscient predator.

In his paper which criticises Charnov's assertion that his deterministic model could be easily extended to a stochastic version, Oaten (1977) also presents his own stochastic model of optimal foraging. Oaten assumes that prey are distributed in patches, with a random number of prey in each patch. The predator does not know without searching how many prey a given patch has, but he does know the distribution of the number of prey per patch and he knows the joint distribution of the time for finding the best stopping rule is described by Green (1979), who finds the stopping rules and the resulting rates of finding prey for a variety of parameter values. The main results are that the best leaving rule is fairly simple, that predators that assess patch quality and use the best stopping rule have a higher rate of finding prey than predators that don't, and that the advantage of assessing patch quality is greatest when patches vary most in quality and the time between patches is shortest.

DISTRIBUTION OF PREY BEFORE PREDATION

In my model I assume that the distribution of prey is a Beta mixture of binomials. If X is the number of prey in a patch then

$$P(X = k) = \binom{n}{k} \frac{\alpha^{[k]}\beta^{[n-k]}}{(\alpha+\beta)^{[n]}} \quad \text{for} \quad k = 0,1,2,\ldots,n$$

where $\binom{n}{k}$ is the number of combinations of n things taken k at a time, $a^{[r]} = a(a+1)(a+2)\ldots(a+r-1)$, n is the number of bits in a patch and α and β are the values that determine the distribution of p. The parameter p has a Beta distribution with parameters α and β. That is,

$$f(p) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} p^{\alpha-1}(1-p)^{\beta-1} \quad \text{for} \quad 0 < p < 1$$

where $\Gamma(\alpha)$ is the Gamma function.

The mean and variance of X are given by

$$EX = n\alpha/(\alpha+\beta),$$

$$\text{Var } X = n\alpha\beta(\alpha+\beta+n)/((\alpha+\beta)^2(\alpha+\beta+1)) .$$

of finding prey as he searches a patch with a known number of prey. The predator knows the time it takes to go from patch to patch and he uses his prior knowledge as well as his experience in a patch to decide when to leave a patch so as to maximize his long term rate of finding prey.

Unfortunately, Oaten's model is too general to be mathematically tractable. I have considered a tractable special case of Oaten's stochastic model of optimal foraging (Green 1979) and have found the best stopping rule and the rate of finding prey for a predator using the best stopping rule for a variety of environmental conditions. In this paper I look at the distribution of prey per patch under my model, at the functional response and, finally, at the distribution of the number of prey in a patch after a visit by an optimal forager.

THE MODEL

The model considered here is a special case of the general stochastic model considered by Oaten (1977). I assume that prey are distributed in patches which are divided into bits, each of which may contain a prey. All patches are assumed to have the same number of bits, but the number of bits containing prey is random. I assume that the number of prey in a patch will have a binomial distribution with n equal to the number of bits and p being random, having a Beta distribution with parameters α and β. The values of α and β determine the distribution of the number of prey per patch. Smaller values of α and β mean that the number of prey per patch is more variable.

An optimal (Bayesian) forager decides when to stop searching and leave a patch based on his knowledge of α, β, n, the average time between patches, τ, and his experience in the present patch. The method

Notice that if we keep n and $\alpha/(\alpha+\beta)$ fixed $(\alpha/(\alpha+\beta) = P$, say) then the mean will remain the same but that

a) as $\alpha,\beta \dashrightarrow 0$ Var X $\dashrightarrow n^2P(1-P)$, and

b) as $\alpha,\beta \dashrightarrow \infty$ Var X $\dashrightarrow nP(1-P)$.

Case a) corresponds to a 2-point limiting distribution where all patches either have no prey at all or they have prey in every bit, while case b) corresponds to a binomial distribution.

All the calculations given in this paper are done for $n = 20$ and $\alpha/(\alpha+\beta) = P = .25$. The effect of the variability of the environment is included by varying α and β.

The distribution of the number of prey per patch is given in the following table for each of several sets of values for the parameters α and β. Variances are also given.

Table 1

The Beta-binomial distribution, $n = 20$, $P = .25$

($\beta = 3\alpha$). Values in table for $P(X = k)$.

k	$\alpha = .25$	$\alpha = .5$	$\alpha = 1$	$\alpha = 2$	$\alpha = 4$
0	.3841	.2448	.1304	.0598	.0261
1	.0972	.1194	.1186	.0957	.0673
2	.0616	.0873	.1073	.1137	.1065
3	.0468	.0707	.0966	.1186	.1322
4	.0386	.0601	.0864	.1146	.1405
5	.0334	.0525	.0768	.1048	.1332
6	.0297	.0466	.0678	.0917	.1153
7	.0270	.0417	.0593	.0772	.0922
8	.0249	.0377	.0514	.0627	.0687
9	.0233	.0342	.0440	.0492	.0478
10	.0221	.0310	.0373	.0372	.0311
11	.0211	.0282	.0311	.0271	.0188
12	.0204	.0256	.0254	.0188	.0106
13	.0198	.0232	.0203	.0125	.0055
14	.0194	.0209	.0158	.0078	.0026
15	.0193	.0186	.0119	.0045	.0011
16	.0193	.0164	.0085	.0024	.0004
17	.0197	.0141	.0056	.0011	.0001
18	.0206	.0118	.0034	.0004	.0000
19	.0226	.0092	.0017	.0001	.0000
20	.0290	.0060	.0006	.0000	.0000
Var X	39.375	27.500	18.000	11.667	7.941

THE STOPPING RULE

For a given distribution of the number of prey per patch and a given average time between patches (measured in the same units as the time to search one bit within a patch) there exists a stopping rule that maximizes the long term rate of finding prey. For each possible number k, of prey found, $k=0,1,2,\ldots,n$, there will be a time $t(k)$ such that the predator will leave the patch if it has found only k prey at time $t(k)$. The method for finding the best stopping rule is given by Green (1979).

Two examples of stopping rules are given below. The cases are similar in that the patches are the same size $(n = 20)$, are of the same average quality $(\alpha/(\alpha+\beta) = .25)$, and the average time between patches is the same $(\tau = 1)$. However, in one case $(\alpha = .25, \beta = .75)$ the patch quality is more variable than in the other $(\alpha \doteq 2, \beta = 6)$.

Table 2 shows the stopping rules for each case and gives the probabilities of finding particular numbers of prey in each case. Notice that when patches vary more in quality the predator leaves a patch more readily ($t(k)$ is smaller). In the table, k stands for the number of prey caught when the predator leaves the patch, $t(k)$ is the stopping time for k prey, $p(k)$ is the probability of finding k prey, EG and Var G are the mean and variance of the number of prey caught in a patch, ES and Var S are the mean and variance of the number of bits searched and R is the long term rate of finding prey.

Table 2

Stopping Rules and Probability of Finding a Given Number of Prey

	Case a) α = .25, β = .75		Case b) α = 2, β = 6	
k	t(k)	p(k)	t(k)	p(k)
0	1	.7500	2	.5833
1	3	.0547	5	.1273
2	5	.0188	9	.0404
3	7	.0094	12	.0267
4	9	.0057	15	.0182
5	11	.0038	17	.0181
6	13	.0027	20	.0112
7	15	.0020	20	.0247
8	16	.0031	20	.0309
9	18	.0017	20	.0301
10	19	.0026	20	.0261
11	20	.0030	20	.0209
12	20	.0076	20	.0156
13	20	.0099	20	.0110
14	20	.0117	20	.0071
15	20	.0132	20	.0043
16	20	.0148	20	.0023
17	20	.0164	20	.0011
18	20	.0184	20	.0004
19	20	.0215	20	.0001
20	20	.0290	20	.0000
EG	2.7093		2.2625	
ES	4.2720		6.7875	
Var G	36.1152		14.9153	
Var S	46.2431		50.2814	
R	.5139		.2905	

Table 2 shows that when patch quality varies more the number of prey captured using the best stopping rule also varies more than when patch quality is more uniform. The average number of prey captured in each case is about the same, but the average amount of time per patch is greater in the less variable patches.

The effect of changes in patch variability may be seen by considering more cases, each with the same patch size $(n = 20)$, average quality $(\alpha/(\alpha+\beta) = .25)$ and time between patches $(\tau = 1)$, but with different values of α. Smaller values of α mean more variable patch quality.

Table 3 gives values of EG, ES and R for various values of α. The average number of prey captured is greatest for highly variable patches and for patches that vary hardly at all. There is a fairly wide range of degrees of variability (values of α) for which there is little difference in the average number of prey captured per patch. The average time spent per patch tends to increase as patch variability decreases. The long term rate of capturing prey decreases steadily with decreasing variability in patch quality.

Table 3

Average number of prey captured, EG, average number of bits searched, ES, and long term rate of finding prey, R, for n = 20 bits, $\tau = 1$ and $\beta = 3\alpha$, for various values of α.

α	EG	ES	$R = EG/(ES+\tau)$
.05	4.1273	5.1191	.6745
.1	3.6171	4.8200	.6215
.15	3.2449	4.6078	.5786
.2	2.9462	4.4217	.5434
.25	2.7093	4.2720	.5139
.3	2.5167	4.1494	.4887
.4	2.3802	4.2963	.4494
.5	2.2005	4.2432	.4197
.6	2.0755	4.2370	.3963
.7	1.9513	4.1677	.3776
.8	1.8661	4.1533	.3621
.9	1.7840	4.1101	.3491
1.0	2.5143	6.4195	.3389
2.0	2.2625	6.7875	.2905
3.0	2.6850	8.9071	.2710
4.0	2.6369	9.0880	.2614
5.0	2.7371	9.7172	.2554
6.0	3.0646	11.1859	.2515
7.0	3.1616	11.7086	.2488
8.0	3.1731	11.8589	.2468
10.0	3.4290	13.0494	.2441
12.0	3.6180	13.9265	.2424
16.0	3.9087	15.2526	.2405
20.0	4.1841	16.4677	.2395
30.0	4.5665	18.1428	.2386
40.0	4.7736	19.0363	.2382
50.0	4.8968	19.5623	.2381
100.0	5.0000	20.0000	.2381

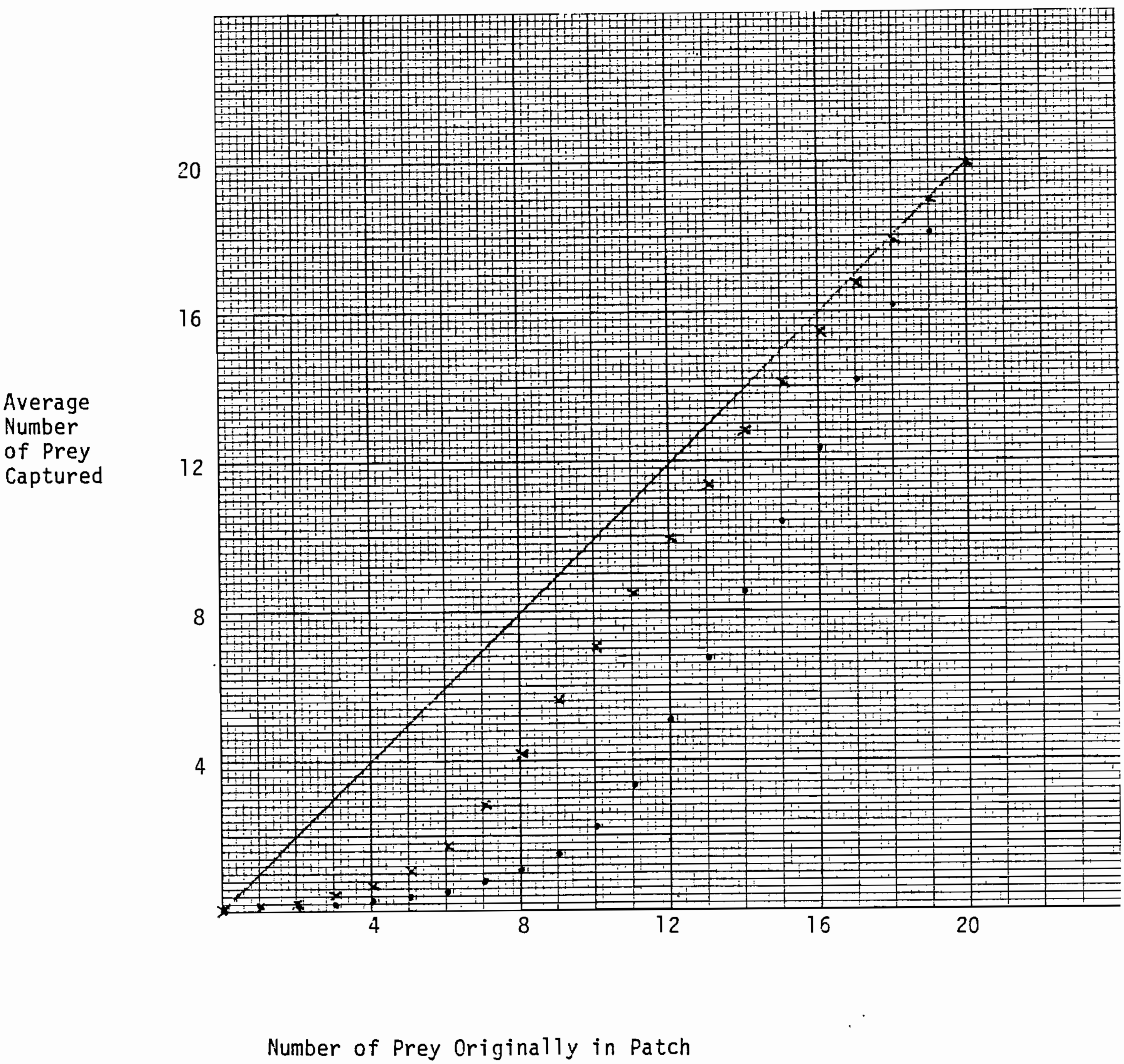
Figure 1: Functional Response

Average number of prey found in a patch plotted against the number of prey in the patch. In both cases, $\alpha/(\alpha+\beta) = .25$, $n = 20$, $\tau = 1$.

. $\alpha = .25$, $\beta = .75$

x $\alpha = 2$, $\beta = 6$

Solid line represents capturing every prey in the patch.



FUNCTIONAL RESPONSE

For this stochastic model the number of prey captured in a patch is not uniquely determined by the number of prey in the patch. The location of the prey in the patch is also important. When the predator uses the best stopping rule it will tend to stay a shorter time in patches with fewer prey.

For a patch with a given number of prey we can calculate the expected number of prey captured in that patch by a predator that uses the optimal stopping rule. When the number of prey expected to be captured in a patch originally containing a given number of prey is plotted against that given number a convex curve is seen (see Figure 1). This curve resembles the first part of a Type III functional response curve. In my model the predator searches systematically at a constant rate and does not become satiated. It should be noted that I consider the number of prey taken per patch, not the number of prey taken per unit time. It is considering the number of prey taken per unit time that produces the flattening usually seen in the functional response curve.

Once the best stopping rule $t(k)$; $k = 0,1,\ldots,n$ has been found for a given distribution of the number of prey per patch, the distribution of the number of prey captured using that best rule when searching a patch with a known number of prey can be found. If the patch is known to contain j prey the number of ways of stopping after finding exactly i prey, where $i \leq j$, is $w(i)x(i,j)$, where $w(i)$ is the number of ways of getting to the stopping point $(t(i),i)$, given by

$$w(i) = \binom{t(i)}{i} - \sum_{l=0}^{i-1} w(l) \binom{t(i)-t(l)}{i-l}$$

where $w(0) = 1$, and $x(i,j)$ is the number of ways of getting from the stopping point $(t(i),i)$ to the point (n,j). Here $x(i,j)$ is given by

$$x(i,j) = \binom{n-t(i)}{j-i} .$$

The probability of finding exactly i prey in a patch originally containing j prey is $P(i|j) = w(i)x(i,j)/\binom{n}{j}$.

The functional response is calculated by finding the average number of prey taken for a patch with j prey in it, namely,

$$EX = \sum_{i=1}^{j} iP(i|j) .$$

Table 4 gives the functional response for a predator using the best stopping rule for several cases where patches are of size $n = 20$, the bits are of average quality $\alpha/(\alpha+\beta) = .25$ and the time between patches is $\tau = 1$. Lower values of α mean more variable patches.

In all cases the average number of prey taken per patch increases slowly as a function of the number of prey present at first but as the number of prey present becomes larger the average number of prey found increases more rapidly until for patches full of prey all the prey are taken.

When the functional response is compared for different degrees of patch variability it is seen that for less variable patches (higher values of α) the number of prey taken per patch is closer to the average number of prey in the patch. This is because the optimal predator tends to stay longer in each patch when patches vary less in quality. This may be seen in Table 4 and in Figure 1.

Table 4

Functional response. For various prey distributions (values of α) with $\beta = 3\alpha$, $n = 20$, the average number of prey taken in a patch originally containing k prey, for a Bayesian predator using the best stopping rule when $\tau = 1$ is the time between patches.

k	$\alpha = .25$	$\alpha = .5$	$\alpha = 1$	$\alpha = 2$	$\alpha = 4$
1	.05	.05	.1	.1	.15
2	.1105	.1158	.2316	.2316	.3474
3	.1851	.2026	.4044	.4167	.6263
4	.2788	.3201	.6374	.6902	1.0392
5	.3996	.4838	.9669	1.1128	1.6756
6	.5594	.7184	1.4527	1.7718	2.7033
7	.7799	1.0641	2.2136	2.8534	4.1742
8	1.0953	1.5897	3.4491	4.2139	5.6966
9	1.5630	2.4206	4.9900	5.6427	7.1915
10	2.2805	3.6807	6.6139	7.0827	8.6289
11	3.3915	5.0766	8.2366	8.5358	10.0043
12	5.0499	6.5161	9.8178	9.9871	11.3142
13	6.7799	7.9962	11.3418	11.4213	12.5586
14	8.5599	9.5251	12.7961	12.8243	13.7403
15	10.3996	11.1064	14.1776	14.1834	14.8657
16	12.2788	12.7418	15.4885	15.4885	15.9439
17	14.1851	14.4360	16.7316	16.7316	16.9851
18	16.1105	16.2	17.9053	17.9053	18
19	18.05	18.05	19	19	19
20	20	20	20	20	20

DISTRIBUTION OF PREY AFTER PREDATION

One thing that can be seen by examining Table 4 is that on the average, more prey will be left after predation in those patches originally containing an intermediate number of prey than in patches originally containing a very large or a very small number of prey. This is because while most prey are left for poor patches, there are few prey to leave, while better patches are profitable to stay in and a predator using the best stopping rule will be likely to exhaust them.

This suggests that predation by an optimal predator tends to stabilize the number of prey per patch. It is possible to compare the distribution of the number of prey remaining in patches after predation by predators using the best stopping rule with the distribution of the number of prey that would remain if the same proportion of prey were removed from the patches at random. When this comparison is made it is seen that while the mean number of prey per patch is the same for each type of removal of prey, the patches visited by optimal predators will be more variable, not less. This is seen by comparing Table 5 and 6.

Table 5 gives the distribution of the number of prey per patch after each patch has been searched by a predator using the optimal stopping rule for patches originally having a Beta-binomial distribution of number of prey per patch. Means and variances are also given.

Table 6 gives the distribution of the number of prey per patch after randomly removing the same overall proportion of prey as would be removed by a predator using the best stopping rule. For a patch originally having k prey the number remaining after random removal will have a binomial

Table 5

The distribution of the number of prey, X, remaining in a patch after a search by a Bayesian predator. Values in the table are for P(X = k) for various values of α, for $\beta = 3\alpha$, n = 20 and $\tau = 1$.

k	α = .25	α = .5	α = 1	α = 2	α = 4
0	.5378	.3900	.3325	.2751	.3109
1	.1039	.1310	.1461	.1331	.1267
2	.0672	.0967	.1271	.1372	.1422
3	.0517	.0769	.1047	.1216	.1316
4	.0421	.0622	.0826	.0993	.1053
5	.0351	.0506	.0628	.0764	.0754
6	.0296	.0411	.0464	.0558	.0490
7	.0251	.0334	.0333	.0388	.0292
8	.0212	.0271	.0232	.0258	.0159
9	.0178	.0218	.0157	.0163	.0079
10	.0149	.0175	.0103	.0098	.0036
11	.0124	.0139	.0066	.0055	.0015
12	.0103	.0109	.0040	.0029	.0005
13	.0084	.0085	.0023	.0014	.0002
14	.0068	.0064	.0013	.0006	.0000
15	.0054	.0047	.0006	.0002	.0000
16	.0042	.0033	.0003	.0001	.0000
17	.0031	.0021	.0001	.0000	.0000
18	.0021	.0012	.0000	.0000	.0000
19	.0011	.0005	.0000	.0000	.0000
20	.0000	.0000	.0000	.0000	.0000
EX	2.2907	2.7995	2.4857	2.7375	2.3631
Var X	13.6915	13.0142	7.6697	7.1765	5.3792

Table 6

The distribution of the number of prey, Y, left in a patch after randomly removing the proportion that would be removed by a Bayesian predator. Values in the table are for $P(Y = k)$ for various values of α, for $\beta = 3\alpha$, $n = 20$ and $\tau = 1$. The overall proportion of prey originally in a patch left after random removal is given by p_1.

	$\alpha = .25$	$\alpha = .5$	$\alpha = 1$	$\alpha = 2$	$\alpha = 4$
k p_1:	.45814	.55990	.49714	.54750	.47262
0	.4687	.3239	.2394	.1455	.1310
1	.1208	.1546	.1960	.1939	.2251
2	.0782	.1101	.1573	.1881	.2306
3	.0612	.0866	.1231	.1569	.1797
4	.0521	.0710	.0935	.1181	.1160
5	.0466	.0592	.0685	.0818	.0645
6	.0422	.0495	.0480	.0524	.0315
7	.0376	.0409	.0319	.0311	.0137
8	.0317	.0330	.0199	.0171	.0053
9	.0246	.0256	.0115	.0086	.0018
10	.0170	.0186	.0060	.0040	.0006
11	.0103	.0125	.0029	.0017	.0002
12	.0054	.0075	.0012	.0007	.0000
13	.0024	.0040	.0004	.0002	.0000
14	.0009	.0018	.0001	.0001	.0000
15	.0003	.0007	.0000	.0000	.0000
16	.0001	.0002	.0000	.0000	.0000
17	.0000	.0001	.0000	.0000	.0000
18	.0000	.0000	.0000	.0000	.0000
19	.0000	.0000	.0000	.0000	.0000
20	.0000	.0000	.0000	.0000	.0000
EY	2.2907	2.7995	2.4857	2.7375	2.3631
Var Y	9.5057	9.8530	5.6986	4.7359	3.0201

distribution with parameters k and p_1, where p_1 is the overall proportion of prey left in patches after each patch has been visited by an optimal predator. Comparison of Tables 5 and 6 show that seemingly paradoxical result that the variance in the number of prey per patch after predation by an optimal predator is greater than after random removal of prey from patches.

The explanation of this seeming paradox is that while optimal predators do, on the average, remove a larger fraction of the prey from patches originally with a larger number of prey they do this by removing all or a large number of prey from most patches containing a large number of prey, but they leave all or nearly all of the prey in a few such dense patches. Random removal, on the other hand, is unlikely to remove all of the prey from a dense patch, but it is not likely to leave all or nearly all of the prey in a dense patch either. The reason that patches searched by optimal predators have a larger variance than patches from which prey have been removed at random is that occasionally the optimal predator will leave a good patch too soon. In a sense, an agent that removes prey at random (by "acts of God", for example) can never leave a patch too soon.

In Charnov's (1976) model the predator searches a patch randomly until the rate of finding prey falls to the highest level that can be maintained over a long period of time. All patches are thus reduced to the same quality. No mechanism has been proposed that could produce such a result. The predators would have to be omniscient. In my model the predator searches systematically (without searching the same bit twice) until he exhausts the patch or decides that the patch is not very good.

The stopping rule that such a predator should use is quite simple and just depends on how many prey have been found in the patch in a certain amount of time. The effect of an optimal (Bayesian) predator, however, is not to stabilize the prey distribution between patches. After being searched by an optimal forager patches will vary slightly more in number of prey than they would if they had been searched at random by a predator using the fixed time stopping rule (see Hassell and Southwood 1978).

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