ANALYSIS OF A SELECTIVE PREDATION EXPERIMENT

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Avian responses to objects in their environments may be affected greatly by the object's color. A conventional signaling system may be involved, as when parent birds respond to the color of the gape of nestlings or when a pattern on the beak of the parent elicits a pecking response in the chick. Adults may react to the bright color of poisonous insects or of edible fruits: thus avian behavior patterns have led to the evolution of a wide variety of aposematic and mimetic insects. Distasteful insects and edible fruits very often show the same range of colors—reds and yellows. The difference lies in the response of the birds, which varies between species and is subject to modification as a result of experience and association. Several investigators have shown that when birds are presented with a choice of food of two or more types, they may tend to eat more than proportionately the kind of which they have had most experience or which appears most common during the course of the experiment (Allen and Clarke 1968; Coppinger 1969; O'Donald and Pilecki 1970; Tinbergen 1960). It seems likely that these results reflect optimal feeding strategy of the predators. The form the strategy may take has been discussed in some detail (Holling 1965; Royama 1970; Rapport 1971). We are not concerned here with the response as a behavioral problem, but rather with whether it can be demonstrated in another bird species and with the effect it may have on a prey species. Predators consistently selecting the more common of two morphs of a species may maintain a polymorphism. Selection on the prey is frequency dependent, and the result has been called apostatic polymorphism (Clarke 1962) because visually distinct forms are favored. In principle, this behavior also tends to increase the number of morphs in a population, and in so doing may decrease the average intensity of predation, so that density interacts with mean relative fitness. Such multiple polymorphisms have not been studied experimentally.

The experiment to be described is one of a series designed to investigate the response of birds to a choice of colored foods under different conditions of frequency, density, and number of morphs. The predators are Japanese

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quail, *Coturnix coturnix japonica* Temminck and Schlegel, and the "prey" consists of colored pastry pellets. Results illustrate a new method of analysis that appears suitable for comparative studies of predator behavior.

Quail feed for the most part on grain and plant shoots but in the breeding season expand their diet to include insects. Their preferences could, therefore, influence morph frequencies in insect species. Whether or not quail are important selective agents for any prey, it is valuable to have comparative data from a variety of bird species concerning their response to color-choice situations.

MATERIALS AND METHODS

Experiments were carried out in a controlled artificial environment using fully mature Japanese quail, between 8 and 12 weeks old, supplied by High Garth Hatcheries, Leatherhead Road, Great Bookham, Surrey. Birds were kept in pairs in small holding cages between experiments and transferred during a trial to an aviary with a 2 m $\times$ 2 m sawdust-covered floor and wooden walls 2 m high. This arena was strongly illuminated with artificial light. Trials commenced at the same time each day.

Prey consisted of cylinders, 1 mm in diameter and 2 cm long, of raw pastry dyed red or blue. These colors were chosen because Taylor, Sluckin, and Hewitt (1969) found no innate preference for either color in Japanese quail chicks. When possible, experiments were carried out using male-female pairs as predators, although occasionally a pair of males was used because we could not always obtain enough females. Single birds cannot be used because they panic and become nervous when left alone.

A number (N) of prey, consisting of R (reds) and B (blues) were scattered on the floor of the aviary. The quail were then introduced and kept under continuous observation until 50% of the prey were eaten. The birds were then removed, and the time was noted. Ten pairs were tested at each frequency of the two colors of prey investigated, and each pair repeated the trial 10 times on successive days.

Table 1 shows how results were compiled and some of our notation. In all experiments N was 20 and R was 2, 4, 6, 8, 10, 13, or 16. Table 2 (discussed fully below) contains data on total numbers of each color taken per trial.

TABLE 1

NOTATION USED IN DESCRIBING A PREDATION EXPERIMENT, SHOWING NUMBERS OF THE TWO CLASSES PRESENTED, EATEN, AND REMAINING ON A SINGLE DAY

	Presented	Eaten	Not Eaten	No. Remaining at Given Point during Course of Experiment
Red type	R	r^1	r	l
Blue type	B	b^1	b	m
	N	$Y = N/2$	Z	...

The value μ is the mean number of red prey left per day (i.e., of r). Thus quail pair 37 gave rise to $\mu = 4.5$, indicating that over 10 successive days 45 red prey were uneaten. For the 10 days, $N = 200$ and the frequency of red presented was 40%. A total of 80 red prey were put out, of which 45 remained. Hence 120 blues were presented, and since there is always 50% predation, 55 of these were uneaten.

RESULTS AND METHOD OF ANALYSIS

Results of experiments are summarized in table 2, together with estimates derived from them. Estimated values were calculated using a simple model of predator behavior, which assumes that birds confronted with l red and m blue prey act so that the probability of the next prey removed being red is

$$P_R = \frac{l}{l + am}, \tag{1}$$

and the probability of its being blue is

$$P_B = \frac{am}{l + am}. \tag{2}$$

Here a is a positive quantity reflecting predator selectivity.

If $a = 1$, then $P_R = l/(l + m)$ and $P_B = m/(l + m)$, and predators exert no preference but are equally likely to choose any one of the $l + m$ available prey. If $a = 1/2$, then $P_R = 2l/(2l + m)$, and the predators act as if they see half as many blue prey (or twice as many red prey) as are really present.

To estimate a from data in table 2, we use an approximate relationship between μ, the expected mean daily value of r, and the value with which the predators act (see Appendix for derivation). This is

$$a = \frac{\log\ [B/(Z - \mu)]}{\log\ (R/\mu)}. \tag{3}$$

The values R, B, and Z are, respectively, the numbers of the two colors presented and the total number not eaten, on each day.

When the two types of prey are equally frequent, $P_R = 1/(1 + a)$, for all frequencies. The expression

$$\beta = \frac{1}{(1 + a)} \tag{4}$$

is therefore the probability that the first prey taken is a red, if the predators act in the same way with 50% presentation as they do at the experimental frequency. This provides a convenient probabilistic interpretation of the a value.

Predators with no visual discrimination between the two morphs have $a = 1$ and $\beta = 0.5$ at all frequencies of presentation. The graph of β on the

TABLE 2

RESULTS OF EXPERIMENTS AND ESTIMATES DERIVED FROM THEM

Red (%)	Pair No.	$\hat{\mu}$	$\tilde{\sigma}$	$\hat{\alpha}$	95% Confidence Limits for α	$\hat{\beta}$
10	1	1.5	0.71	2.63	1.00–∞	0.28
	2	1.8	0.42	7.60	2.63–∞	0.12
	3	1.7	0.48	4.67	2.06–∞	0.18
	4	0.9	0.74	0.86	0.39–2.06	0.54
	5	1.3	0.95	1.68	0.54–∞	0.37
	6	1.6	0.70	3.40	1.17–∞	0.23
	7	0.6	0.70	0.54	0.20–1.17	0.65
	8	1.0	0.82	1.00	0.39–3.40	0.50
	9	1.0	0.67	1.00	0.46–2.63	0.50
	10	0.9	0.82	0.85	0.30–2.96	0.54
20	11	3.7	0.48	12.30	5.33–∞	0.08
	12	2.5	0.97	1.61	0.84–3.82	0.38
	13	0.9	1.00	0.38	0.16–0.70	0.72
	14	1.5	0.97	0.64	0.35–1.20	0.61
	15	2.2	1.03	1.20	0.64–2.51	0.45
	16	1.2	0.92	0.50	0.25–0.92	0.67
	17	2.3	0.16	1.32	0.64–3.29	0.43
	18	2.6	0.84	1.78	1.00–3.82	0.36
	19	1.4	1.18	0.65	0.28–1.20	0.61
	20	1.3	1.06	0.54	0.25–1.10	0.65
30	21	2.3	1.06	0.62	0.36–1.07	0.62
	22	3.0	0.82	1.00	0.67–1.52	0.50
	23	3.2	1.55	1.15	0.54–2.71	0.47
	24	3.8	0.92	1.79	1.07–3.33	0.36
	25	1.6	1.18	0.39	0.21–0.67	0.72
	26	5.9	0.32	76.30	2.33–∞	0.01
	27	3.2	0.63	1.15	0.82–1.65	0.47
	28	3.8	1.03	1.79	1.07–3.33	0.36
	29	4.0	0.94	2.09	1.27–3.98	0.32
	30	2.0	1.33	0.51	0.25–1.00	0.66
40	31	3.5	1.18	0.74	0.46–1.20	0.58
	32	4.0	1.56	1.00	0.51–2.00	0.50
	33	5.9	1.66	3.53	1.53–11.9	0.22
	34	1.7	1.70	0.24	0.08–0.51	0.81
	35	3.3	1.57	0.66	0.33–1.28	0.60
	36	3.1	0.57	0.58	0.46–0.74	0.63
	37	4.5	1.27	1.35	0.79–2.45	0.43
	38	5.7	2.83	3.04	0.84–44.9	0.25
	39	3.5	1.35	0.74	0.40–1.35	0.58
	40	4.2	1.75	1.13	0.51–2.63	0.47
50	41	4.7	0.82	0.84	0.59–1.19	0.54
	42	0.0	0.00	0.00	0.00–0.00	1.00
	43	3.5	1.51	0.41	0.19–0.79	0.71
	44	3.7	0.82	0.46	0.32–0.67	0.68
	45	6.0	1.33	1.79	1.00–3.37	0.36
	46	4.5	1.18	0.75	0.47–1.19	0.57
	47	4.2	1.40	0.63	0.34–1.12	0.61
	48	4.8	1.03	0.89	0.59–1.33	0.53
	49	4.7	2.00	0.84	0.36–1.91	0.54
	50	3.9	1.85	0.52	0.22–1.12	0.66
65	51	6.4	0.97	0.94	0.59–1.45	0.52
	52	4.0	1.16	0.13	0.02–0.30	0.89
	53	5.3	1.34	0.44	0.19–0.86	0.69
	54	4.7	1.16	0.27	0.11–0.51	0.79
	55	4.6	0.70	0.25	0.15–0.38	0.80
	56	6.3	2.16	0.88	0.29–2.33	0.53
	57	5.9	1.00	0.68	0.41–1.07	0.60
	58	3.9	1.66	0.11	0.00–0.38	0.90
	59	5.6	1.58	0.55	0.23–1.13	0.64
	60	6.0	1.83	0.72	0.27–1.65	0.58

TABLE 2 (*Continued*)

Red (%)	Pair No.	$\hat{\mu}$	$\hat{\sigma}$	$\hat{\alpha}$	95% Confidence Limits for α	$\hat{\beta}$
80	61	7.9	1.27	0.75	0.30–2.01	0.57
	62	6.3	1.40	0.08	0.00–0.50	0.92
	63	7.0	2.67	0.35	0.00–2.20	0.74
	64	6.4	1.60	0.11	0.00–0.62	0.89
	65	7.5	2.00	0.62	0.03–0.93	0.62
	66	6.4	0.93	0.11	0.00–0.39	0.89
	67	7.4	2.00	0.56	0.00–2.01	0.64
	68	6.0	0.00	0.00	0.00–0.00	1.00
	69	7.4	2.00	0.56	0.00–2.01	0.64
	70	6.5	1.67	0.15	0.00–0.76	0.87

frequency of type A presented is then a horizontal straight line at $\beta = 0.5$. If predators discriminate between morphs in a frequency-independent manner, that is, if they have a definite color preference or the colors are not equally visible, then values of α and β are constant and the regression of β on frequency is a horizontal straight line above 0.5 (preference for red morphs) or below 0.5 (preference for blue morphs). If predators always favor rare morphs, the regression of β on the frequency of A presented has a positive slope. The curve's shape indicates the relation between frequency and predator response. The form of individual trials and the method of analysis are outlined below.

A pair of quail (pair number 51 in table 2) was presented with 13 red and seven blue pellets on each of 10 consecutive days. Each day they were allowed to eat 10. Consequently $R = 13$, $B = 7$, and $Y = Z = 10$. The numbers of red prey remaining after each experiment (values of r) were: 6, 6, 6, 5, 6, 6, 7, 6, 8, 8.

If we assume the behavior of the birds was consistent over the 10 days, these values can be regarded as a random sample from a population with a mean μ and a standard deviation σ. Estimates of μ and σ^2 are then $\hat{\mu} = \Sigma_i r_i / 10 = 6.4$ and $\hat{\sigma}^2 = \Sigma_i (r_i - \hat{\mu})^2 / 9 = 0.9333$, where r_i represents the r value on the ith day. Substituting $\mu = 6.4$ into equation (3), together with $X = 7$, $W = 13$, and $Z = 10$, gives $\hat{\alpha} = 0.94$. From equation (4) the corresponding value of β is $\hat{\beta} = 0.52$.

Now, if we regard the r values as a random sample from an approximately normal distribution (see Appendix) with a mean μ and standard deviation σ, confidence limits for μ are of the form $\mu \pm t\hat{\sigma}/\sqrt{10}$. The value of t at the required confidence level is found from the t table with 9 degrees of freedom. For the example, the 95% confidence limits of μ are 5.7 to 7.1. These, of course, include the value 6.5 which is the expectation based on the assumption of proportional removal. Substitution of the confidence intervals in equation (3) gives limits for α of 0.59–1.46 and for β of 0.41–0.63.

To obtain confidence limits for μ, α, and β, we used the estimate of σ obtained by repeating the basic predation experiment. Should experimental repeats not be possible, a value for σ can be obtained by solving equations (3a) and (5a) in the Appendix.

<center>DISCUSSION</center>

<center>*Quail Behavior*</center>

Experiments were designed to test whether quail without prior conditioning behave in a frequency-dependent manner over a range of frequencies. If the effect is to under-eat the rare form whatever its color, compared with the frequency of presentation, then the quail could exert pressure tending to maintain a polymorphism in a variable prey species. Polymorphisms that could be maintained this way occur in insects and molluscs, which have avian predators. Although animals form only a small part of the quail diet, it is of interest to know how widespread the behavior pattern is among birds. Results summarized in table 2 and displayed in figures 1 and 2 show conclusively that quail do behave appropriately. The value of β, the preference for red prey, is less than 0.5 at low frequencies of red presented and greater than 0.5 at high frequencies. Using a distribution-free test of the differences in the mean level of groups of observations (Quenouille 1959), we obtain
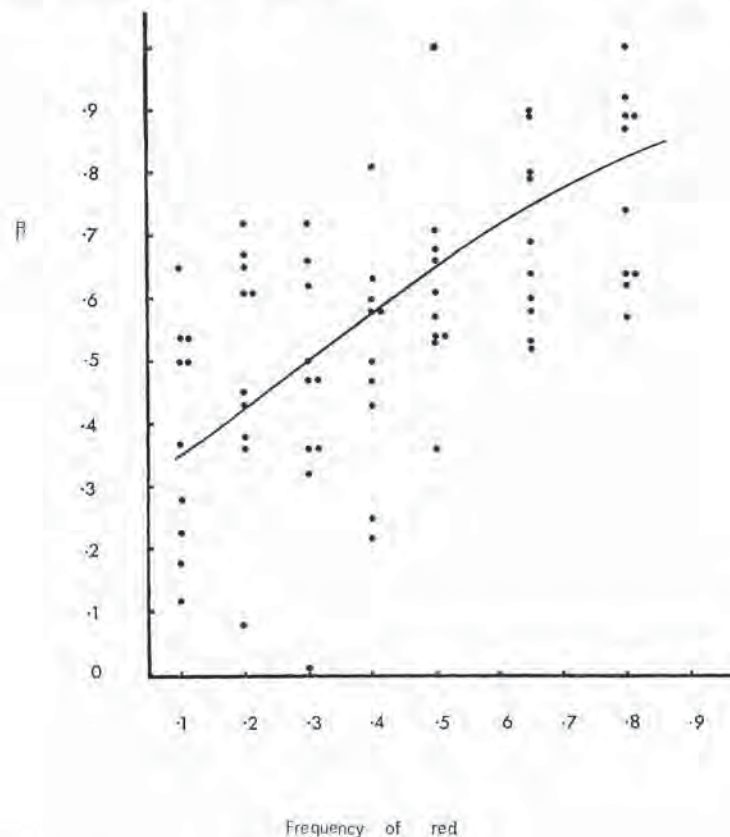

Frequency of red

FIG. 1.—Mean values of β, the probability that the next prey taken was red if both prey were present at equal frequencies, plotted against frequency of red. The fitted curve is described in the text.
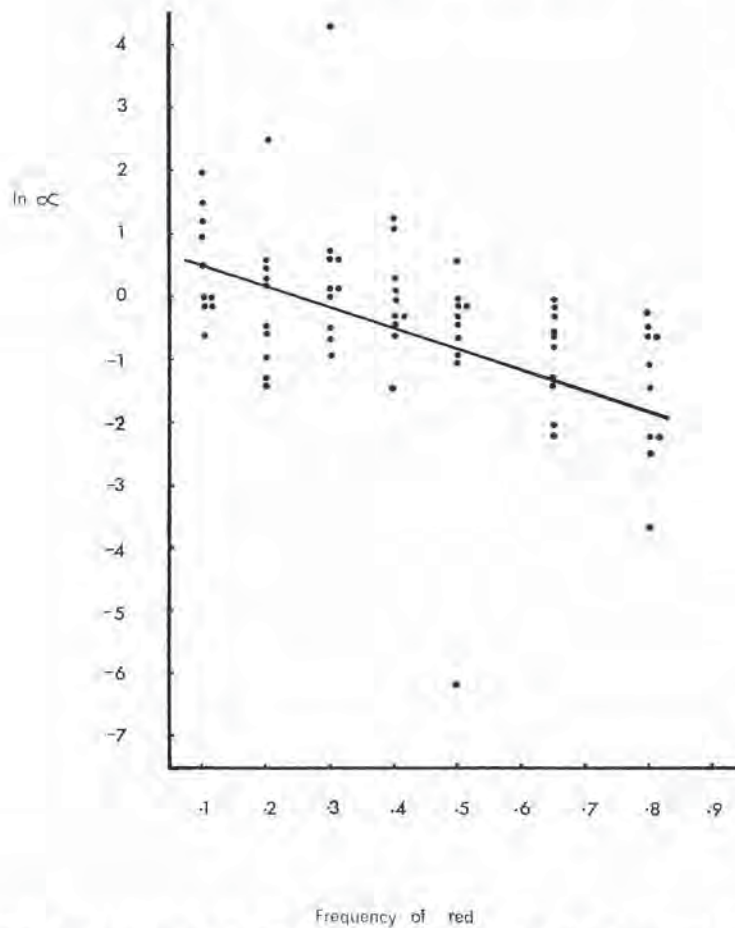
Frequency of red

Fig. 2.—Relation of the logarithm of the selective index to frequency of red presented.

$x_6^2 = 21.3$ $(P \simeq .001)$, showing that the trend is significant. The data also indicate a tendency to remove more reds than expected on the assumption of equal visibility and acceptability of prey. This effect and the tendency to apostatic selection are superimposed. If both colors are equally visible and acceptable, the mean frequency of reds taken at 50% presentation should be 50% even though there is apostatic selection; β should be 0.5. In fact, only one trial gave rise to a value of β below 0.5 while nine were above it and the mean value is 0.60. The probability of obtaining this result by chance is 0.02. At 40% presentation the mean value of β is 0.51. It drops to 0.45 at 30%, then rises again to 0.50 at 20% presentation. The variation is no doubt due to chance factors, but apparent equality of acceptance of the two colors clearly occurs at a point somewhere below 40% presentation. The strength of the difference in visibility of, or preference for, the colors may be measured by finding the presentation frequency at which $\beta = 0.5$, for at this value the

birds cannot be exerting any frequency-dependent preference (see Elton and Greenwood 1970). It is of interest, therefore, to consider models which describe the change in preference with frequency.

For apostatic selection to occur, β must increase and α decrease with frequency. The index α is a factor describing the number of times the predator is more likely to select one color rather than the other. As such, it is a ratio varying about one from zero to infinity. The asymmetry of the distribution is seen in calculated values (table 2). It may be removed by taking instead the logarithm of α; figure 2 shows the regression of $\ln \alpha$ on frequency of presentation. Two pairs (nos. 42 and 68) had α values of zero. These were adjusted by increasing by one the total number of blues eaten and reds uneaten, so that $\alpha = 0.1$ in the one instance and 6.1 in the other. The trend is reasonably linear and thus accords with the simple hypothesis that the degree to which the predator is more likely to select one color than the other changes exponentially with frequency over the range studied. The calculated regression line has a slope of $b = -3.047$, with a y intercept of $a = 0.917$.

If we accept this relation between α and frequency, then the change in β with frequency is given by the logistic equation $\beta = 1/(1 + Ke^{bp})$, where p is the frequency of presentation and $K = e^a$. The curve is shown in figure 1. Using these calculated parameters, $\beta = 0.5$ when $p = 0.301$. The frequency-independent preference for red may, therefore, be represented by the factor $(1 - p)/p = 2.32$, indicating that quail are 2.3 times more likely to take red than blue, irrespective of frequency. The value b measures the strength of the tendency for selection to change with frequency of presentation, and may be used as an index of that strength when comparing results of different experiments.

The strong red color preference of the quail was unexpected, since Taylor, Slukin, and Hewitt (1969) found no evidence of an innate preference for red or blue in quail chicks. A difference between coloring fluids in smell or flavor seems unlikely. The quantity used was very small compared with the quantity of pastry in the prey pellets, and the fluids are tasteless and odorless to human senses. The hatcheries from which the birds came have been visited, and there was no sign there of any influences in the rearing environment that would lead to color selection. It is possible that the red preference develops with maturity. Turcek (1963) found that a variety of seed- and fruit-eating birds favored red food. This preference may be related to the fact that red is frequently associated with ripe fruits. Birds are very sensitive to red hues, to judge from their commonness among aposematic insects. Response to red in particular could be advantageous in active mature individuals, whereas early innate preferences for a variety of colors may be associated with the releasing colors of the parental beak or throat in species that spend an appreciable time helpless in a nest. The bright color of ripe fruits may have arisen because it attracts the attention of birds and facilitates seed dispersal. If so, frequency-dependent behavior as observed here would promote uniformity of color, just as the learned association of color and distastefulness promotes uniformity in Müllerian mimics.

Analytical Method

Studies on this problem have begun from one of three starting points: (*a*) the value of the behavior to a predator (Tinbergen 1960; Holling 1965; Mueller 1971; Rapport 1971; Tullock 1971); (*b*) the coexistence of separate prey species as a result of density-dependent predation (Williamson 1957; Murdoch 1969); or (*c*) the coexistence of polymorphs within a species as a result of frequency-dependent predation (Clarke 1962; Moment 1962; Croze 1970; Greenwood 1969). When considering the population dynamics of pairs of species or variates, we naturally think in terms of numbers (or densities). So far as the genetics of a polymorphic system is concerned, however, change in density is not the first consideration and may not even be relevant, and it is more natural to discuss the phenomenon in terms of frequencies. This is the usual way of approaching other genetic systems, although it is by no means necessary—thus Haldane and Jayakar (1963 and elsewhere) have obtained useful solutions in population genetics by studying ratios.

It is easier to work with frequencies because they vary only from zero to one, rather than from zero to infinity. Unfortunately, the relation between the situations before and after selection under constant selection, which is linear on the ratio scale, becomes curved on the frequency scale. The selective factor to be found is the same in either case, being a proportionality constant relating the frequency or ratio before selection to that after it. The present measure, α, differs from those used previously, since it is derived from a probabilistic rather than a deterministic model. It will have the same mean value as an equivalent deterministic selective value, but has the advantage that it correctly estimates the amount of selection when a substantial fraction of a finite population is predated, whereas the deterministic factor gives an underestimate. As derived, it varies inversely with preference—a value less than one indicates that reds are preferred—while β varies directly with preference.

Several methods have been employed in the analysis of selection experiments. It is appropriate, therefore, to consider their relationship and to justify the development of a new and somewhat more complex one. In all cases the results of an experiment may be expressed as the totals selected from two or more categories. Numerical treatment of these totals is required to test the significance of a difference from expectation, or of heterogeneity, and to provide a measure of the selective pressure exerted. The required calculations are simple, but the assumptions on which they are based vary from one experiment to another in ways that are not always obvious. We may recognize the following categories of result.

a) Experiments have been conducted (Brower and Brower 1965, and earlier) in which the forms to be compared are displayed to the predator in pairs in a series of repeated presentations. The overall frequency taken may then be compared with the frequency presented. Suppose there are two types, A and B, presented at a frequency ϕ of A. If p is the frequency of A taken in a total of Y, then $\chi^2 = (p - \phi)^2 / \text{Var}_p$. Var_p is the binomial variance

$p(1 - p)/Y$. This is equivalent to the simple χ^2 test comparing observed and expected numbers in the two categories. A straightforward measure of selectivity is the cross-product ratio A_1B_0/A_0B_1, the subscripts referring to the presented and the selected series, which is the same as our estimate α. The situation is essentially the same in the experiment of Allen and Clarke (1968), where predators were presented with 200 prey at a time, replaced during the experiment to keep the frequency available as constant as possible. Of course, modification of the analysis may be required to allow for heterogeneity with time or for a more complex experimental procedure, etc.

b) In the other main category of results the data fall into a two-by-two table. In some instances, observations have been made in nature from which selection may be inferred. Thus, random samples of two or more color morphs of the snail *Cepaea nemoralis* have been compared with samples taken by thrushes (Cain and Sheppard 1954). Under certain circumstances the marginal totals of the contingency table, which represent the ratio of the two morphs and the ratio of predated to unpredated individuals, may both be random variables. Differential selection between human collector and bird may be tested by the χ^2 test of heterogeneity, and a measure of selectivity is the cross-product ratio of frequency taken by birds and frequency present overall in the table. It may or may not be the same as α, depending on the effect the predators have on the composition of the population.

Similar data from human populations are discussed by Woolf (1955). He uses the logarithm of the cross-product ratio, since it is symmetrically distributed, and derives a significance test using its variance. The comparison made is between the numbers of two classes of individuals affected by a disease (analogous to the numbers of the two classes of *Cepaea* in a predated sample) and the numbers of the two classes present in the population at large. Since some members of the population sample may have the disease, whereas the population sample of snails will not contain predated individuals, Woolf's test is not the same as the two-by-two χ^2 test and will not usually be applicable. The appropriate test of significance using the logarithm of the cross-product ratio is provided by Edwards (1965).

Another experimental procedure is to take a fixed number of individuals of two classes and compare variability within them. For example, 100 males and 100 females might be scored for frequencies of particular blood groups. (The collector of *Cepaea* samples is probably also more likely to adopt this procedure than the one described above.) The test of significance of difference in frequency is not strictly the two-by-two χ^2 test of heterogeneity (Rahman 1968). Instead, if p_1 is the frequency of the blood group in males and p_2, the frequency in females, we should find $\chi^2 = (p_1 - p_2)^2/(\text{Var}_{p_1} + \text{Var}_{p_2})$. The two variances would be binomial. In practice, this adjustment makes very little difference. The subject of the two-by-two situation is discussed in detail by Sokal and Rohlf (1969), including the approach via the likelihood ratio test G.

c) A third category of observations is that in which samples of two classes of prey are presented to predators, which take an appreciable fraction of the total before the results of their activity are studied. Sometimes predators

may be seen removing prey (Turner 1961; Morrell and Turner 1970; O'Donald and Pilecki 1970), so that each class of prey consists of two categories: those eaten and those not eaten. The investigator may stop the experiment near some preferred frequency eaten, but the total number removed is likely to be a random variable. Since the frequency available changes during the course of the experiment, the appropriate test of significance is the χ^2 test comparing frequency eaten with frequency presented at the start (situation 1), but using the hypergeometric variance (O'Donald and Pilecki 1970). If the numbers in the different categories are represented as in table 1, this is given by $\chi^2 = (r^1N - RY)^2 (N - 1)/RBYZ$. An approximately similar value may be obtained by calculating χ^2 from the double-binomial model mentioned in the paragraph above. If there is 50% presentation of the two classes and 50% of the total is eaten, the result is greater than the χ^2 value based on the hypergeometric distribution by a factor of $N/(N - 1)$. Other frequencies of presentation and predation give slightly different discrepancies: the difference is not great so long as N is reasonably large.

d) A related situation is one where different classes of a living organism are released in the wild and selective predation is inferred from their frequencies among the recaptured sample. The best-known experiments of this kind are those of Kettlewell (1956, and earlier) on typical and melanic morphs of the moth *Biston betularia*. Another series was designed by L. P. Brower and others to test for differential response of wild birds to mimics and their controls (Cook, Brower, and Alcock 1969, and earlier). If we only know the frequency recaptured after the conclusion of the experiment but not the frequency actually eaten, then both the degree of selectivity of predators and the standard error of the estimated selectivity require different treatment. The estimate of selection exerted by predators is affected by the intensity of predation; the simple algebra of the situation is discussed by Cook (1971). The standard error is modified because there may be random variation in mortality of the two classes, and so of the proportion recaptured, even in the absence of selection by predators (Manly 1972).

The value α has been derived for use in experiments, such as the one described, where the proportion of the two classes presented and the fraction taken are both fixed. It may also be applied when there is some variation in the fraction eaten, and can be obtained directly from the frequency of one class that remains uneaten. It provides a true measure of predator behavior unaffected by finite population size. An adequate estimate of the standard error of α can also be derived, which is not influenced by variation in starting frequency or by small population size. It is therefore preferred over other possible estimates as an index of predator selection in this type of experiment.

SUMMARY

A new index of selection, α, is presented. It measures the degree to which a predator is more likely to take one kind of prey rather than another, and

thus provides a direct estimation of predator behavior. It is unaffected by sampling in a finite population, this being the advantage over other methods of estimating selectivity.

If selection is independent of the frequency of prey types, α is constant. Under frequency-dependent predation α changes with frequency. Measures of the frequency-independent and the frequency-dependent components may be obtained when both kinds of selection act together.

The method of analysis has been applied to data on the behavior of Japanese quail, *Coturnix coturnix japonica*, presented with red and blue pastry food under controlled conditions. Variability in response between individual pairs of birds is large. A strong red preference is nevertheless exhibited, and also a distinct tendency for the birds to eat more than a proportional amount of whichever color was the most common over a range of frequencies from 10% to 80% red. Behavior of this kind would favor a stable equilibrium in a polymorphic animal prey species, and uniformity of color in edible fruits if the bird acts as a beneficial agent of dispersal.

APPENDIX

Assume a predation experiment is being carried out and a total of i prey have been removed by the predators (table A1). This can only arise if either (a) when $i-1$ prey were removed there were g of color A left and the ith prey was of color B, or (b) when $i-1$ prey were removed there were $g+1$ of color A left and the ith prey was of color A. Let

$$\Theta_i(g) = g/\{g + \alpha(N - i - g)\} \tag{1a}$$

denote the probability that the $(i+1)$th prey is of color A, given the situation in table A1. Also let $P_i(g)$ denote the probability that the situation of table 3 will arise during the experiment. It can then be shown that the equations

$$P_i(g) = [1 - \Theta_{i-1}(g)] P_{i-1}(g) + \Theta_{i-1}(g + 1) P_{i-1}(g + 1), N \geqslant i \geqslant 1,$$
$$P_0(g) = \begin{cases} 1, g = R, \\ 0, g < R, \end{cases} \tag{2a}$$

TABLE A1
SITUATION AFTER i PREY HAVE BEEN REMOVED

Prey	Total	Removed	Not Removed
Color A	R	$R - g$	g
Color B	B	$i + g - R$	$N - i - g$
Total	N	i	$N - i$

will hold because there are only two ways (a and b, above) of reaching the situation of table 3. Equations (2a) can be used to evaluate $P_1(g)$ ($g = R - 1$, R), then $P_2(g)$ ($g = R - 2$, $R - 1$, R), and so on up to $P_Y(g)$, where Y is the number of prey taken when the experiment stops (table 1). Since $P_Y(g)$ is the probability that r takes the value g, the distribution of r can be obtained for any value of α. Values of μ and σ, the mean and standard deviation of r, can therefore be calculated. Unless N is very small, an electronic computer will be required for these calculations. The full distribution of r is usually not required for analysis of predation experiments. Let μ_i and σ_i be the mean and standard deviation of g when i prey have been removed. Interest then centers on μ_Y and σ_Y, which are usually denoted by μ and σ. Multiplying both sides of equation (2a) by

$$[g(1 - \alpha) + \alpha(N - i + 1)][g + 1 + \alpha(N - i - g)]$$

gives the equation

$$[g(1 - \alpha) + \alpha(N - i + 1)] \; [g + 1 + \alpha(N - i - g)] \, P_i(g)$$
$$= \alpha(N - i + 1 - g) \; [g + 1 + \alpha(N - i - g)] \, P_{i-1}(g)$$
$$+ (g + 1)\alpha(N - i + 1 - g) \, P_{i-1}(g + 1).$$

Summing both sides of this equation for values of g in the range $N - i$ to R, remembering that $P_i(g)$ is zero outside the range $(N - i, R)$ then produces

$$(1 - \alpha)^2 \sum_{N-i}^{R} g^2 P_i(g) + (1 - \alpha)\,[(1 - \alpha)$$
$$+ 2\alpha(N - i + 1)] \sum_{N-i}^{R} g P_i(g)$$
$$+ \alpha(N - i + 1)[1 - \alpha + \alpha(N - i + 1)] \sum_{N-i}^{R} P_i(g)$$
$$= -\alpha(1 - \alpha) \sum_{N-i+1}^{R} g^2 P_{i-1}(g)$$
$$+ [\alpha(N - i + 1)(1 - \alpha) - \alpha(1 - \alpha)$$
$$- \alpha^2(N - i + 1)] \sum_{N-i+1}^{R} g P_{i-1}(g)$$
$$+ \alpha(N - i + 1)[1 - \alpha + \alpha(N - i + 1)] \sum_{N-i+1}^{R} P_i(g)$$
$$+ (1 - \alpha) \sum_{N-i+1}^{R-1} (g + 1)^2 P_{i-1}(g + 1)$$
$$+ [\alpha(N - i + 1) - 1 + \alpha] \sum_{N-i+1}^{R-1} (g + 1) P_{i-1}(g + 1).$$

It then follows that

$$(1 - \alpha)^2 \, (\sigma_i{}^2 + \mu_i{}^2) + (1 - \alpha)\,[(1 - \alpha)$$
$$+ 2\alpha(N - i + 1)] \; \mu_i + \alpha(N - i + 1) \; [1 - \alpha + \alpha(N - i + 1)]$$
$$= -\alpha(1 - \alpha)\,(\sigma_{i-1}{}^2 + \mu_{i-1}{}^2)$$
$$+ [\alpha(N - i + 1) \; (1 - \alpha) - \alpha(1 - \alpha) - \alpha^2(N - i + 1)] \; \mu_{i-1}$$

$$+ \alpha(N - i + 1) \ [1 - \alpha + a(N - i + 1)]$$
$$+ (1 - \alpha)(\sigma_{i-1}^2 + \mu_{i-1}^2)$$
$$+ [\alpha(N - i + 1) - 1 + \alpha] \ \mu_{i-1},$$

which reduces to

$$(1 - \alpha) \ (\sigma_i^2 + \mu_i^2) + [2\alpha(N - i) + 1 + \alpha] \ \mu_i$$
$$= (1 - \alpha) \ (\sigma_{i-1}^2 + \mu_{i-1}^2) + [2\alpha(N - i + 1)$$
$$+ 1 + \alpha] \ \mu_{i-1} - 2(1 + \alpha) \ \mu_{i-1}. \quad (3a)$$

Denoting the left-hand side of this equation by H_i, we see that

$$H_i = H_{i-1} - 2(1 + \alpha)\mu_{i-1}$$
$$= H_{i-2} - 2(1 + \alpha)\mu_{i-2} - 2(1 + \alpha)\mu_{i-1}$$
$$= H_0 - 2(1 + \alpha) \sum_0^{i-1} \mu_s.$$

But

$$H_0 = (1 - \alpha)(\sigma_0^2 + \mu_0^2) + (2\alpha N + 1 + \alpha)\mu_0$$
$$= (1 - \alpha) \ R^2 + (2\alpha N + 1 + \alpha) \ R,$$

since $\sigma_0 = 0$ and $\mu_0 = R$. Equation (3a) therefore becomes

$$(1 - \alpha)\sigma_i^2 = (1 - \alpha) \ (R^2 - \mu_i^2) + (2\alpha N + 1 + \alpha) \ (R - \mu_i)$$
$$- 2(1 + \alpha) \sum_0^i \mu_s + 2(1 + \alpha + \alpha i) \ \mu_i, \quad (4a)$$

which relates σ_i to $\mu_0, \mu_1, \ldots, \mu_i$. Returning to equations (2a) we see that

$$g \ P_i(g) = [1 - \Theta_{i-1}(g)] \ g \ P_{i-1}(g) + \Theta_{i-1} \ (g + 1) \ g \ P_{i-1} \ (g + 1).$$

Hence

$$\sum_{N-i}^R g \ P_i(g) = \sum_{N-i+1}^R g \ P_{i-1}(g) - \sum_{N-i+1}^R g \ \Theta_{i-1}(g) \ P_{i-1}(g)$$
$$+ \sum_{N-i}^{R-1} (g + 1) \ \Theta_{i-1}(g + 1) \ P_{i-1}(g + 1)$$
$$- \sum_{N-i}^{R-1} \Theta_{i-1}(g + 1) \ P_{i-1}(g + 1).$$

Therefore

$$\mu_i = \mu_{i-1} - \sum_{N-i+1}^R g \ \Theta_{i-1}(g) \ P_{i-1}(g) + \sum_{N-i+1}^R g \ \Theta_{i-1}(g) \ P_{i-1}(g)$$
$$- \sum_{N-i+1}^R \Theta_{i-1}(g) \ P_{i-1}(g)$$

so that

$$\mu_i = \mu_{i-1} - \sum_{N-i+1}^R \Theta_{i-1}(g) \ P_{i-1}(g).$$

If $\theta_{i-1}(g)$ is now expanded in a Taylor series about $g = \mu_{i-1}$, and only the first three terms are substituted into the right-hand side of this equation, then we have the approximation

$$\mu_i = \mu_{i-1} - \Theta_{i-1}(\mu_{i-1})$$
$$+ \frac{(1-\alpha)\,\Theta_{i-1}{}^2\,(\mu_{i-1})}{\mu_{i-1}{}^2}\,\{1 - (1-\alpha)\,\Theta_{i-1}(\mu_{i-1})\}\sigma_{i-1}{}^2, \quad (5a)$$

relating μ_i to μ_{i-1} and σ_{i-1}. Equations (4a) and (5a) can now be used to evaluate successively $\mu_1, \sigma_1, \mu_2, \sigma_2, \ldots, \mu_Y, \sigma_Y$ by noting that $\mu_0 = R$ and $\sigma_0 = 0$. A simpler method of obtaining the means, μ_i, which, although more approximate, is quite accurate, is found by noting that the third term on the right-hand side of equation (5a) is small when μ_{i-1} is large. Assuming this is the case, we have

$$\mu_i = \mu_{i-1} - \Theta_{i-1}(\mu_{i-1}).$$

Writing $t = i/N$, $\delta t = 1/N$ and $U_t = \mu_i/N$, this becomes

$$U_t = U_{t-\delta t} - \frac{U_{t-\delta t}}{U_{t-\delta t} + \alpha(1 - t + \delta t - U_{t-\delta t})}\,\delta t$$

or

$$\frac{U_t - U_{t-\delta t}}{\delta t} = - \frac{U_{t-\delta t}}{U_{t-\delta t} + \alpha(1 - t + \delta t - U_{t-\delta t})}.$$

Taking the limit as $N \to \infty$ gives

$$\frac{dU}{dt} = - \frac{U}{U + \alpha(1 - t - U)},$$

which has the solution

$$\frac{1 - U - t}{1 - R/N} = \left(\frac{U}{R/N}\right)^{\alpha}$$

if boundary condition $U = R/N$ when $t = 0$ is applied. In the earlier notation this solution is

$$\frac{N - \mu_i - i}{B} = \left(\frac{\mu_i}{R}\right)^{\alpha} \qquad (6a)$$

from which equation (3) follows. Equation (3) is therefore an approximation appropriate for large values of N. Equation (6a) is remarkably accurate considering the approximations that have led to it. Some numerical comparisons of equation (6a) and the exact values of μ found by solving equations (2a) are given in table A2.

When $\alpha = 1$, equations (4a) and (5a) do not yield the values of σ_i. However, in this case of no selection the situation is really that of hypergeometric sampling; and it can be shown that

$$\mu_i = \frac{R(N - i)}{N}$$

and

$$\sigma_i{}^2 = \frac{RBi(N - i)}{N^2(N - 1)}.$$

TABLE A2

A COMPARISON OF THE APPROXIMATIONS DERIVED FOR THE MEAN, μ, AND STANDARD DEVIATION, σ, OF r

R	α	μ			σ	
		Exact	Approx.*	Approx.†	Exact	Approx.*
10	0.90	4.815	4.815	4.181	1.146	1.146
	0.70	4.375	4.375	4.385	1.140	1.140
	0.50	3.801	3.801	3.820	1.121	1.122
	0.30	2.989	2.988	3.019	1.072	1.074
	0.10	1.600	1.599	1.649	0.907	0.908
6	10.00	5.395	5.395	5.371	0.699	0.695
	3.33	4.550	4.550	4.527	0.938	0.935
	2.00	3.961	3.961	3.946	1.012	1.010
	1.43	3.515	3.515	3.506	1.041	1.040
	1.11	3.155	3.155	3.152	1.050	1.051
	0.90	2.843	2.843	2.846	1.050	1.051
	0.70	2.465	2.465	2.473	1.040	1.041
	0.50	1.961	1.961	1.973	1.007	1.010
	0.30	1.243	1.242	1.252	0.908	0.916
	0.10	0.225	0.249	0.174	0.470	0.376
2	10.00	1.853	1.853	1.848	0.367	0.366
	3.33	1.599	1.599	1.592	0.557	0.555
	2.00	1.390	1.390	1.384	0.637	0.635
	1.43	1.215	1.215	1.211	0.673	0.672
	1.11	1.066	1.066	1.065	0.687	0.686
	0.90	0.932	0.933	0.934	0.687	0.687
	0.70	0.768	0.768	0.770	0.671	0.671
	0.50	0.549	0.549	0.551	0.619	0.617
	0.30	0.265	0.267	0.258	0.476	0.453
	0.10	0.014	0.011	0.006	0.118	0.053

NOTE.—All of the results in this table refer to experiments with $Y = 10$ and $N = 20$.
* Approximations to μ and σ obtained using equations (4a) and (5a).
† Approximations to μ obtained using equations (6a).

When $i = Y$ we therefore obtain

$$\mu = ZR/N \tag{7a}$$

and

$$\sigma^2 = RBYZ/[N^2(N-1)]. \tag{8a}$$

In obtaining confidence limits for μ the formula

$$\mu \pm t\,\hat{\sigma}/\sqrt{10}$$

has been suggested. In using limits of this form the assumption is being made that r has a near-normal "shape" of distribution. With N as small as 20, as in the experiments of this paper, this assumption only holds when R and B are both close to $\frac{1}{2}N$ and α is close to unity. When these conditions do not apply (particularly in the experiments with $R = 2$), these confidence limits must be regarded as being very approximate.

Table A2 gives a comparison between various exact values of μ and σ, and the approximations to these obtained with the equations derived above. The approximations are clearly least accurate when R is small and α is very small. Results not reported here show that when N is larger than 20, the approximations produce even better accuracy. Tables of the σ values corresponding to a large range of N, R, and B values are being prepared. These should prove useful when it is not possible to repeat the basic experiment often enough to produce a good standard-error estimate.

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