Switching in General Predators: Experiments on Predator Specificity and Stability of Prey Populations
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SWITCHING IN GENERAL PREDATORS: EXPERIMENTS ON PREDATOR SPECIFICITY AND STABILITY OF PREY POPULATIONS[1]

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Abstract. "Switching" in predators which attack several prey species potentially can stabilize the numbers in prey populations. In switching, the number of attacks upon a species is disproportionately large when the species is abundant relative to other prey, and disproportionately small when the species is relatively rare. The null case for two prey species can be written: $P_1/P_2 = cN_1/N_2$, where P_1/P_2 is the ratio of the two prey expected in the diet, N_1/N_2 is the ratio given and c is a proportionality constant. Predators were sea-shore snails and prey were mussels and barnacles.

Experiments in the laboratory modelled aspects of various natural situations. When the predator had a strong preference (c) between prey the data and the "null case" model were in good agreement. Preference could not be altered by subjecting predators to training regimens. When preference was weak the data did not fit the model and replicates were variable. Predators could be trained easily to one or other prey species. From a number of experiments it was concluded that in the weak-preference case no switch would occur in nature except where there is an opportunity for predators to become trained to the abundant species. A patchy distribution of the abundant prey could provide this opportunity.

Given one prey species, snails caused a decreasing percentage mortality as prey numbers increased. This occurred also with 2 prey species present when preference was strong. When preference was weak the form of the response was unclear. When switching occurred the percentage prey mortality increased with prey density, giving potentially stabilizing mortality. The consequences of these conclusions for prey population regulation and for diversity are discussed.

Introduction

If the density of some populations is relatively stable over several generations two explanations are available. First, the populations themselves may possess stabilizing mechanisms, or second, the stability may be imposed upon them by the community they live in. These possibilities are not mutually exclusive. That general predators act as mechanisms of the second type is an eminently reasonable notion which has been present in the literature for many years (e.g., Elton 1927, p. 122; Moore 1967, p. 109). Such predators attack a variety of prey and the idea is that they tend to feed most heavily upon the most abundant species. As this particular prey species declines in numbers, partly owing to the predation, the predator "switches" the great proportion of its attacks to another prey which has become the most abundant. In this way no prey population is drastically reduced nor is any prey species allowed to become very abundant.

It seems strange that this idea has remained so imprecise. The absolute amount of predatory mortality required to stabilize the abundant prey and the capacity of the predator to cause such mortality must be known before the idea can be examined adequately, and these in turn require information about prey rates of increase and about the "functional" and "numerical" responses of the predator (Solomon 1949). (The way the number of prey eaten per predator changes as a function of prey density is the functional response;

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the way the number of predators changes is the numerical response). A complete analysis of the idea, requiring the integration of these various facets of predation, is complex and requires extensive treatment. I will deal here only with the problem of "switching"; that is, given that both prey are eaten when presented alone to a predator, does the predator switch from the one prey when it becomes rare to the other which is more abundant? Since this question is the central part of the idea of the stabilizing mechanism, it seems appropriate to answer it first. It should be remembered, however, that before switching produces stability it must result in an increasing percentage of mortality in any prey species as this prey increases in density.

I wanted to know if the properties necessary for switching were shown by a particular predator-prey system, and I built an experimental model using predatory sea-shore snails and their prey. I did not try to see if the snails switch in natural situations. Negative results would not imply necessarily that the snails do not switch in nature nor would positive results necessarily imply that switching does occur in nature. But from the idea I deduced that we should find evidence for the capacity to switch, and this study was designed to look for this evidence.

I examined two situations. In the first the predators' diets show a strong bias in favor of one of the two prey species ("strong preference"); in the second, the diets of predators show weak bias ("weak preference").

The study looked at the relationships among preference, training and switching, and between switching and functional response. In this paper I try to show that where preference was strong snails did not become trained, did not switch, and caused mortality of a kind which would not stabilize prey numbers. Where preference was weak snails were easily trained and, under some circumstances, these two features combined to produce switching; the switching resulted in potentially stabilizing mortality upon the prey.

Throughout the paper the use of behavioral terms has been unavoidable. They are used naively and descriptively and imply nothing about either the theories or the semantics of that subject.

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THEORY: A CRITERION FOR SWITCHING

I consider here experiments in which two prey species are presented to one predator species. The first requirement is a criterion for switching, and this involves establishing a "null case," that is, the expected results in the absence of switching. Essentially this null case is a simple model of predation. Various approaches are possible, such as deriving the null case from more general predation models, but the simplest criterion seemed to be that the expected ratio of the two prey species in the diet (the food eaten), P_1/P_2, should be proportional to the ratio in the food offered, i.e.

$$P_1/P_2 = c\,N_1/N_2, \qquad (1)$$

where N_1/N_2 is the ratio given and c is a proportionality constant.

In the simplest case the two prey species are attacked at the same rate, $c = 1$, and the expected ratio in the diet is the ratio given and the expected line has slope 1 (Fig. 1). When the diets are biased in favor of one of the prey species the line has slope $c \neq 1$. In this case the constant c can be defined as the ratio observed in the diet, P_1/P_2, when the two prey species are equally common in the food given. If there is no switch and the values lie on a straight line (Fig. 1) then the slope of the line which gives the best fit to the points and passes through the origin is an estimate of c.

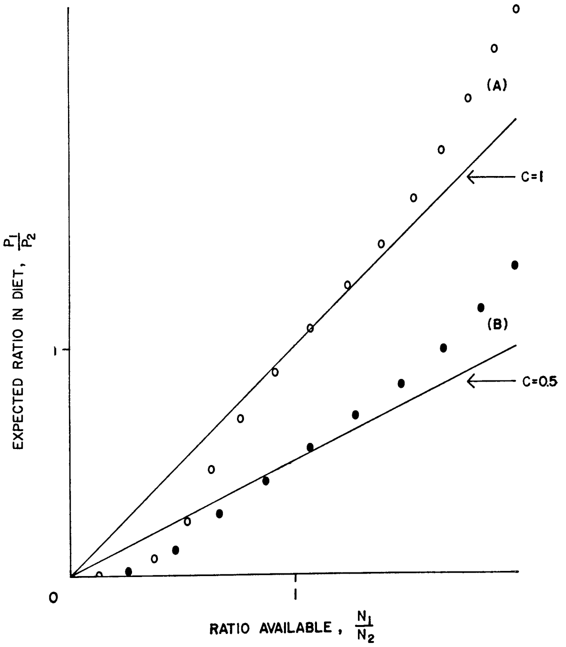

FIG. 1. An illustration of the model presented in theory section. The solid lines indicate expected ratios in the case of no switching, (A) when there is no preference, (B) when species 2 is preferred over species 1. The open and closed circles illustrate the general form of expected ratios when switching occurs.

In the upper curve of Fig. 1 (case A), switching occurs when the more abundant prey forms a higher proportion of the diet than it does of the food available. For case B (Fig. 1) one could demand a similar condition for switching, but I have required only that the observed ratios in the diet lie above and below the predicted line at high and low values of the ratio, N_1/N_2, respectively. In the figure the curves of values representing switching are required to intersect the expected (solid) lines at the point $N_1/N_2 = 1$, since the idea of switching, as expressed by previous authors, requires that in a system with two prey species the more abundant species is attacked disproportionately in comparison with the less abundant species. Clearly this requirement cannot be too narrowly defined in practice, and in real situations the curve should cross the line in some restricted interval about the value of $N_1/N_2 = 1$. Further, ratios of N_1/N_2 different from but close to unity might not produce switching, or if switching occurred it might be too slight to detect. In Fig. 1, therefore, the points representing switching lie close to the expected lines near $N_1/N_2 = 1$, and diverge from the lines as the ratios become extreme. In the experiments I have set extreme prey ratios in the neighborhood of 1:5 and 5:1, and the cross-over point is required to lie clearly within these limits.

It should be stressed that the null hypothesis is purely a numerical statement about the expected prey ratios eaten as the ratios present are varied, and no restrictions are set on the behavioral mechanisms which might lead to switching. For example, switching could occur because the relative availability of the two prey changes as N_1/N_2 varies or because the predators' preference changes with N_1/N_2. Also in a given system switching might occur at one prey density but not at another.

Clearly the ratio N_1/N_2 can vary as a result of several kinds of population changes in the prey. In most of my experiments $N_1 + N_2$ was constant, but I see no reason for restricting the concept of switching to this case.

The proportionality constant c has two basic components: the behavior of the prey, which renders it more or less "available," and the behavior of the predator, i.e. its "preference" for a prey species. (Each component, of course, could be further subdivided. For example the proportion of the *available* prey eaten by the predator is the product of the proportion selected for attack and the proportion of these successfully attacked and eaten. However, I will consider here only the two basic components.) Then, c can be viewed as the product of two constants k and e. Thus k, "relative availability" of the prey, denotes the ratio: the fraction of species 1 contacted / the fraction of species 2 contacted; e, predator "preference," denotes the relative proportions of these contacts which result in successful attacks. In the experiments these two constants were empirically indistinguishable, since only the number of prey attacked was counted. However, the experiments were arranged so that it was reasonable to assume (a) that when the two prey species were equally common they were equally available, and (b) that k was constant in each experiment (that is that the *relative* availability of the two species was linearly related to N_1/N_2). Thus k was assumed to be unity and constant.

A system in which these two assumptions are valid has the following two advantages. First, when the two prey species are equally abundant, the ratio in the predators' diet serves as a measure of the predators' preference. For the rest of this paper, therefore, I have used the word "preference" instead of the phrase "a bias in the predators' diet to one prey species." Second, if switching occurs, the mechanisms can be assumed to involve changes in the predators' preference as prey ratios change. Thus, if c varied as N_1/N_2 changed, this would result from a change in the predators' preference (e) and not from changes in the properties of the prey. If the two assumptions are not valid however, they do not affect the validity of tests for switching using the numerical model outlined above. On the other hand, one would not be able to distinguish effects of changes in the prey from changes in predatory behavior.

To summarize, I have defined switching as follows. As a prey species becomes relatively more abundant, switching occurs if the relative amount which that species forms of the predator's diet increases disproportionately in comparison with the expected amount. The expected amount is based on the proportion that the species forms of the food supplied and on the observed diet when both prey are equally common.

The criterion for switching is most easily presented using ratios, and the predicted null case is satisfactorily linear (Fig. 1); but sometimes, for example when the ratio in the diet is undefined, the denominator being 0, it is better to express the datum as the percentage of one species in the total. Thus where X is the percentage of species 1 in the food presented and Y is the predicted percentage of species 1 in the diet, then the model becomes

$$Y = 100\,cX/\,(100 - X + cX) \qquad (2)$$

and the expected values under the null hypothesis of no switching lie on a curve (Fig. 2). For this criterion too, if switching takes place, the percentages should fall below the curve, when species 1 is rarer, and they should occur above the curve when species 1 is the more abundant.

In this work there seemed to be either good agreement between the model and the experimental data, or very poor agreement. In the first case the constant c was estimated by the slope of the regression line of the means of the ratios of numbers eaten on the ratios given, with the constraint that the regression line pass through the origin, since this is implicit in the model. In the second case, where the fit was obviously very poor, this regression will not provide a good estimate. Since I needed an estimate of preference for descriptive purposes only, I defined it as the mean percentage which one species formed of the diet when the snails were given equal numbers of prey.

Since ratios are awkward to work with, the data were handled as percentages, with one exception. This was the case in which mean ratios were required in a regression to obtain an estimate of c. Then the ratios were transformed to percentages, the mean percentage was calculated and then was transformed back to a mean ratio.

EXPERIMENTAL SYSTEMS AND METHODS

The predators were *Thais emarginata* and *Acanthina spirata,* drilling whelks of the California intertidal. These species attack a wide range of molluscs and Crustacea and usually leave drill holes or marks as evidence of their attacks. The prey were mussels (*Mytilus edulis, M. californianus, Septifer bifurcatus*) and the barnacle *Balanus glandula,* which are species commonly occurring in various mixtures on the shore together with the snails. Sometimes these snails appear to play a large part in determining the abundance of barnacles and mussels in nature (Connell 1961a, 1961b, and 1969 in prep.; Harger 1967). The two main systems studied were *Thais* feeding on *M. edulis* and *M. californianus* (strong preference), and *Acanthina* feeding on *M. edulis* and *Balanus glandula* (weak preference).

The *Thais* were all taken from a small rocky point on UCSB Campus (Goleta Point) and the other predator (*Acanthina*) came from a small area of Carpinteria reef 32 km south-east of campus. Normally predators were kept without food in the laboratory for a few days before each experiment. They survived well and the few which died were replaced during the experiment. The mussels were taken either from Goleta Point or from docks at Ventura (50 km south-east of Santa Barbara). All barnacles were taken from the floats at Ventura. They occur on large mussels and these were split open and thoroughly cleaned; all material on the shell was removed except the barnacles needed for the experiment. Each shell had 6 barnacles, except that occasionally pairs of shells with 5 and 7 barnacles were matched.

The predatory snails used were mostly 25-30 mm long, except where predator size was varied experimentally. The mussels were almost always 15-25 mm long (except where prey size was varied intentionally). When *M. edulis* and *Balanus* were used the mussels were 14-22 mm. The largest basal diameter of barnacles ranged from 9-16 mm. For this species these are large barnacles. It was impossible to get enough mussels and barnacles of exactly equal sizes.

Groups of 2 or more snails were used per replicate and experiments generally were run for several weeks to get relatively large numbers of prey eaten. At intervals (generally each week) all prey, live and dead, were replaced. One of two types of container was used in most experiments. One was a rigid transparent plastic box (12 cm × 11 cm × 7 cm deep) with holes drilled for water circulation. The other was an opaque white plastic vegetable collander (approximately a hemisphere of diameter 24 cm, with many holes). These containers were placed in one or more large indoor tanks (experimental "blocks") with flowing well-aerated sea-water. The positions were randomised in the tanks.

Snails leave drill holes or drill marks on prey they have attacked (generally the prey is dead and empty), so no problem arose over unexplained mortality. However, control treatments of prey without predators were run. Only a dozen or so control mussels died among thousands used. Barnacle control mortality was usually nil, but once reached 2.9%. No correction of the data for unexplained mortality was made.

The specific design of experiments will be discussed at the start of each major section in the Results. However, there were some general problems in experimental design which will now be discussed, since they determined how experiments were done. The first three of these problems concern aspects of the particular systems: predatory hunger, prey availability and the predators' feeding history. The fourth problem, prey replacement, is general to predation studies of this type.

Hunger. The snails ate slowly (at most about 4 prey per snail per week but usually fewer), so that generally several predators were used in each container. Hunger does not seem to be relevant to the experiments. Dozens of unfed snails survived for 6 months (*Thais*) to a year (*Acanthina*) with low mortality before they were returned to the shore (see also Wood 1968). In a test experiment, 5 groups of 5 snails which had been starved for a month ate less in a week than did 5 groups of 5 which had been fed continuously during that month. There was no difference in feeding rate between previously fed and unfed snails in another experiment. In the several experiments using snails which had been starved previously for several weeks, there was no consistent pattern in the feeding rates from week to week. Sometimes snails ate more in the first week than in subsequent weeks, but often this trend was reversed or there was no apparent trend. Indeed, when snails which had been starved were placed beside prey, they often moved from them or wandered over many prey in the first hour or so, then left without feeding and sat still for hours on end. In spite of this, snails ate more when given more prey. But this was not because they could not find food at low prey densities. In fact all prey in a container could be contacted within a few hours. When observed, snails contacted more prey than they ate, and frequently glided over almost all the prey present before eating.

Experiments on the snails' functional response showed that the number of prey eaten tended to level off at about a density of 20-30 prey per container. In the switching experiments, therefore, the total density of the two prey species was at or above this "saturation" density. In these experiments the percentage eaten of the total prey given ranged from 4 to 26%. The rarer prey was never completely eaten out in any replicate.

Prey availability. In the experiments I think all prey were available to the snails. Mussels moved a little at the start and formed small clumps, but essentially the snails were faced with patches of prey, one or two individuals deep, and could move over, under, and among them. The prey seemed to have no escape reaction other than to close their shells or opercula. When barnacles and mussels were used some mussels sometimes sat on barnacles, but snails could still be seen getting at the barnacles. The problem of relative availability was examined experimentally (see Results).

Feeding history of predators. The *Thais* on Goleta Point, where the experimental animals were found, have a mixed diet including goosenecked barnacles (*Pollicipes polymerus*), and several other species of barnacles, some *M. edulis* (which are rare here) and some *M. californianus*. All the *Acanthina* used came from an area with an extensive population of the barnacle *Chthamalus* and, when feeding, usually were eating that species. An occasional individual was found attacking small goosenecked barnacles.

Prey replacement. There is a basic problem in designing experiments where the number of prey of one or more species is varied in different treatments and the number of prey eaten over some time interval is recorded. As soon as prey are eaten, the prey density is different and therefore varies throughout the time of the experiment, unless prey are replaced as they are eaten. But if one replaces prey as soon as they are eaten two problems arise. First, if predators in different treatments or replicates feed at different rates, prey will be replaced at different rates. Second, if the more vulnerable individuals within a prey species are eaten, and if the predation rate varies among replicates or treatments, the proportion of more vulnerable individuals will gradually diminish and will diminish most rapidly when the feeding rates are highest. There seems to be no absolutely correct way to solve this problem. I compromised by replacing all prey, not just the dead ones, once a week, a relatively short time interval compared with the predators' feeding rate. Only in the low density treatments of the functional response experiments was a large percentage of the prey eaten. I discuss this in the section of the Results dealing with functional response.

RESULTS

Preference

Strong and weak preferences were established by measuring the ratio of the numbers of 2 prey attacked by predators when equal numbers of prey were given. I believe this is valid since the prey appear to be equally available when equally abundant. In any case, this ratio can serve as an operational measure of preference.

STRONG PREFERENCE. In the several laboratory experiments, both *Thais* and *Acanthina* showed a strong preference for *M. edulis* over *M. californianus* (Table 1). The strong preference was maintained over a range of prey and predator densities. In *Thais* it could not be altered by

TABLE 1. Ratio of *M. californianus* to *M. edulis* eaten in all replicates in various experiments when the predators were given equal numbers of both prey species.

No. of Snails per Replicate	No. of Prey given per replicate per Week	Total No. of Prey Eaten *californianus: edulis*
2 *Thais*	36	13/69
5 *Thais*	20	4/20
5 *Thais*	50	0/25
10 *Thais*	50	6/56
10 *Acanthina*	20	1/30
10 *Acanthina*	20	2/20

using complex containers (boards with obstacles) where *Thais* had to search for prey. On the shore locally *Thais* also seem to prefer *M. edulis* to *M. californianus* (personal observation and Harger, 1967). *Acanthina* is less well studied locally. All 9 species of invertebrate predators which have been studied in this area show a preference for *M. edulis* (Harger, 1967; Landenberger, 1968). As the major "strong preference" situation, I chose *Thais* feeding upon these 2 mussel species, since *Acanthina* hardly ate *M. californianus* when given *M. edulis.* Groups of *Acanthina* were given only *M. edulis* or only *M. californianus.* They ate an average of 25.5 *M. edulis* and 18 *M. californianus* over the same period. Thus the strength of the preference for *M. edulis* observed in the experiments reported above would not be predicted from these relative feeding rates.

WEAK PREFERENCE. Groups of predatory snails of both species show a weak preference, over-all, between two dissimilar prey, the barnacle *Balanus glandula* and the mussel *M. edulis* (Table 2). The direction of the average preference varied among experiments. Each replicate tended to show a more or less strong preference between the two prey species, producing highly significant heterogeneity among replicates (χ^2 test on original numbers).

Since preference was weaker and heterogeneity more marked in *Acanthina* than in *Thais* in the first experiment, *Acanthina* feeding upon *M. edulis* and *Balanus* was chosen as the "weak preference" situation. When *Acanthina* experiments are analyzed through time, it is seen that any one container of snails tended to maintain a similar diet from one census period to the next. (This analysis is postponed to a later section.) I proposed the following hypothesis to account for these observations. Initially each snail has a weak preference between the two prey species. Once it has made its first choice it becomes trained to some extent to the species it ate, and further feeding tends to reinforce this. In an experiment where prey ratio varied, such a training effect could lead to switching since the proportion of predators attacking the abundant species should increase with each subsequent meal (see Appendix).

The data also suggest that the snails in a particular box all tended to have similar diets, or at least that their diets were not independent of each other and that some sort of facilitation among snails occurred. Various experiments designed to test for one possible mechanism gave equivocal results and are not reported.

Two other possible explanations for the heterogeneity are: (a) that there was some corresponding physical heterogeneity in the sea-water tanks. This seems unlikely, and replicates in similar positions produced different results in different experiments. (b) Conceivably about half the population of *Acanthina* sampled were "innately" barnacle feeders while the other half were "innately" mussel feeders. The following analysis argues strongly against this explanation.

TABLE 2. The percentage of barnacles in the diet of groups of snails given equal numbers of *M. edulis* and *Balanus.*

	No. predators and prey per container				
	5 *Thais* 16 Prey	5 *Acanthina* 16 Prey	2 *Acanthina* 36 Prey	2 *Acanthina* 36 Prey	2 *Acanthina* 36 Prey
Replicate 1	14	25	0	17	5
2	38	34	20	19	65
3	38	35	64	35	82
4	46	73	87	36	88
5	59	80	94	45	89
6	—	—	—	89	—
Mean %	39.0	49.4	53.0	40.2	65.8
Total *Balanus* : *M. edulis* eaten in all replicates	88 : 135	112 : 102	80 : 40	73 : 98	63 : 35

TABLE 3. The number of groups (replicates) of *Acanthina* whose diets contained percentages of barnacles falling between certain values. The snails were given equal numbers of mussels and barnacles. The data come from Table 2.

% Barnacles Eaten	No. of Replicates
0–20	5
21–40	5
41–60	1
61–80	4
81–100	6

Since each replicate contained two or more snails, chosen at random, one would expect an approximately binomial distribution of replicates having the two types of snails. Then, assuming that each type fed at about the same rate, the frequency of replicates with a given percentage of barnacles in their diets should be approximately binomial, or the data should at least show a central tendency with most replicates having an intermediate percentage of barnacles in the diet. This is clearly not so (Table 3). The experiments in the next section also show that explanation (b) is probably false.

Training

Groups of snails were fed pure diets of one prey species for periods of 4–9 weeks. In the more general type of test for training, the ratio of two prey species in the diets of groups of "trained" *Thais* and *Acanthina* was compared with (a) the ratio eaten by snails which had been taken directly from the field, (b) with the preferences already established, or (c) with snails kept in the lab but not fed during the training period. The feeding habits of local snails are known so a major purpose was to see if the 'natural' preference could be altered by a training regimen.

STRONG PREFERENCE. *M. californianus* formed a small part of the diet of the snails in nature. Feeding *Thais* and *Acanthina* a pure diet of this less preferred species did not alter their preference from that shown by snails newly removed from the shore. For *Thais,* based on a sample size of $N = 105$, $\chi^2 = 0.057$ $(0.8 < P < 0.9)$. In *Acanthina* the ratios of *M. californianus* to *M. edulis* eaten were 1:36 (trained to *M. californianus*) and 0:45 (not trained).

WEAK PREFERENCE. Table 4 shows the effects upon *Acanthina*'s subsequent diet of a 4-week pure diet of either mussels or barnacles. There was a strong training effect if trained snails are compared either with unfed snails or with the already established "field" preference (see Table 2).

TABLE 4. The diets of pairs of *Acanthina* given 18 of each prey after various training regimens which lasted 4 weeks. Each treatment had 6 replicates.

Training Regimen	Mean (and Range) % Barnacles in Diet	Total No. Eaten Barnacles : Mussels
To Barnacles.....	87.7 (79-100)	130 : 18
Unfed............	40.2 (17-89)	73 : 98
To Mussels.......	6.8 (0-11)	12 : 168

A second type of training experiment was designed to see if individual *Acanthina* had strong "innate" preferences which could not be altered by training. Further, since there was prior evidence that groups of *Acanthina* became trained to either mussels or barnacles during the course of experiments in which they were given those two prey species, the experiment was so constructed that feeding experiences during the test run would not accumulate and effect the measure of the degree of training. Groups of about 100 *Acanthina* were placed in enamelled pans and given an excess of equally abundant mussels and barnacles. They were then examined at short intervals and removed as soon as they had attacked one prey. Those which had attacked barnacles were then divided into two groups, one of which was fed on barnacles for a month and the other fed on mussels. The mussel–eaters were treated similarly. The experiment thus was factorial, one factor being initial preference and the other subsequent diet (training regimen).

Snails from the 4 treatments were marked by making different numbers of small nicks on the edge of the shell. During the test run 25 snails (1 replicate) from each treatment were placed in an enamelled pan with 160 of each prey species. A pan was thus a block and there were 4 such pans. The snails were examined every 2 hr at first, then later every 4 hr, 6 hr and finally every 8 hr. Each snail was removed as soon as it had eaten one prey and the experiment was stopped at the end of 2 weeks, by which time all but 13 snails had eaten. The training effect was highly significant (Table 5). Any "innate" preference was weak. A two-way analysis of variance was done, using both the untransformed percentages of snails eating barnacles (x), and the transformation $2 \arcsin \sqrt{x}$. The F ratios measuring the significance of initial preference were 3.7 and 3.9, respectively, for these two methods. Both give $0.5 < P < 0.1$. Since each pan was a block and there was no block effect, facilitation was

TABLE 5. The percentage of *Acanthina* which ate a barnacle first, when equal numbers of the mussels and barnacles were available. There were four treatments, arranged factorially, and four replicates in each treatment (see text for details). Total sample sizes for each of the four treatments ranged from 95–99.

		Initial preference	
4-week Feeding Regimen	Relicate No.	for Barnacles	for Mussels
Barnacles..........	1	72.0	52.0
	2	72.0	66.7
	3	80.0	73.9
	4	70.0	75.0
Mussels............	1	29.2	12.0
	2	24.0	16.0
	3	26.1	20.0
	4	34.8	33.3

TABLE 6. The percentage of one prey species among the total number of prey individuals touched by pairs of snails, given various ratios of two prey species. Pairs of *Thais* were given a total of 36 *M. edulis* and *M. californianus*. Pairs of *Acanthina* were given a total of 36 *M. edulis* and *Balanus*. All treatments were replicated 4 times.

		Percent		
Thais was predator	*M. edulis* in food offered	16.7	50	83.3
	M. edulis touched (average)	16.3	54.8	80.5
	Range	12–20	44–63	73–88
Acanthina was predator	*M. edulis* in food offered	16.7	50	83.3
	M. edulis touched (average)	20.5	54.0	83.8
	Range	7–31	44–63	80–93

unimportant relative to training. At the start of the experiment, twice as many snails chose barnacles as chose mussels. In another rather similar experiment, not reported here, about half the snails chose mussels. In that experiment a 17-day training regimen gave even stronger effects than shown in Table 5 but less than one-quarter of the snails fed.

Wood (1968, p. 297) showed that, by feeding *Urosalpinx* a pure diet of one or other of two prey species, the snails' "preference" could be altered. Preference was measured by the proportion of a group of snails which moved towards the effluent coming from one prey species in an olfactometer. Initial "preference" had been slight.

Switching

In these experiments the ratio of 2 prey species (N_1/N_2) offered to predators was varied. The "Theory" section outlines the rationale behind the criterion for switching (Figure 1). I noted there that deviations from the model $P_1/P_2 = c\ N_1/N_2$, owing to changes in c as a function of N_1/N_2, could arise either because the relative availability of the 2 prey is not linearly related to N_1/N_2, or because the predators' preference changes with N_1/N_2.

The question of relative availability of the prey was examined in experiments analogous to those in which I looked for switching (described below). In each replicate, pairs of snails were given one of the prey ratios offered in the major switching experiments. The snails were then watched until 16 *different* prey individuals (out of 36 offered) were touched. Sometimes only 15 prey had been touched after about two hours' observation and, if there was a natural break in the snails activity, this number was used. The results are given in Table 6. (Since there were only 6 individuals of the rare prey, the possible range of values was 0–40% and 60–100% *M. edulis* in the 2 extreme treatments, and 0–100% *M. edulis* in the central treatment.) The results show that the 2 species were equally available when equally common, and that the relative availability closely reflected the relative abundance. Other measures of availability, such as the total number of times a prey species was contacted, gave similar results.

Wood (*op. cit.*) found that *Urosalpinx* often showed a tendency to move towards one species of prey out of two species presented in an olfactometer. However, the response appeared to be towards a strongly directional current of water laden with prey effluent. He found that, when currents coming from 2 prey species were mixed, the predators did not show clear responses. The experimental set up I used had no strong water currents, and the prey were mixed and not separated into different compartments, which probably explains the evidence for random encountering of the 2 prey species.

I now turn to the switching experiments themselves (Table 7). The basic design of the experiments, for both *Thais* and *Acanthina,* provided each pair of snails with 36 prey under an upturned collander (experiments 1, 4 and 6, Table 7). In the strong preference section two additional *Thais* experiments were run. In experiment 2, *Thais* were presented with *M. californianus* and *Septifer* (mussel), with prey density constant at 100. In this experiment each replicate had 20 *Thais* chosen at random from one of 2 size classes: 12-17 mm and 18-26 mm. Different prey sizes were incorporated, but not as a factor; each cage contained equal proportions of 5 equally spaced size classes of mussels covering the range of 15–40 mm. In experiment 3 the prey ratio was altered by setting the number of *M. californianus* at 25 and varying the number of *M. edulis* from 5 to

TABLE 7. Design of switching experiments. For further details see text.

Expt. No.	Predator species	Prey Species	Preference	No. per Container		Extreme Prey Ratios	No. of Weeks	No. Replicates per Treatment
				Predators	Prey			
1.........	*Thais*	*edulis* : *californianus*	strong	2	36	30/6 – 6/30	5	5
2.........	*Thais*	*Septifer* : *californianus*	strong	20	100	10/90–90/10	3	3
3.........	*Thais*	*edulis* : *californianus*	strong	10	30–70	5/25–45/25	3	3
4.........	*Acanthina*	*Balanus* : *edulis*	weak	2	36	30/6 – 6/30	4	5
5a........	*Acanthina*	*Balanus* : *edulis*	weak	2	30	24/6 – 6/24	6	5
5b........	*Thais*	*Balanus* : *edulis*	weak	2	30	24/6 – 6/24	6	5
6.........	*Acanthina*	*Balanus* : *edulis*	weak	2	36	30/6 – 6/30	5	6

TABLE 8. (Experiment 1 in Table 7). The expected and observed percentages of *M. edulis* in the diets of pairs of *Thais* which were given various ratios of *M. californianus: M. edulis.* The calculation of expected values is explained in the Theory Section. Each observed value is the mean of 5 replicates.

% *M. edulis* given............	16.7	50	83.3
% *M. edulis* expected..........	41.8	78.2	94.7
% *M. edulis* observed	44.2	84.8	94.6
Range.......................	24–60	72–100	87–100
Total no. prey eaten...........	85	82	117

45. In the weak preference section, experiment 5 was run in cages on rocks on the sea-shore; the prey were all replaced every two weeks, compared with every week in all other experiments. In experiment 6 training of *Acanthina* was introduced as a factor; groups of snails were fed for 4 weeks only *M. edulis,* only *Balanus glandula* or nothing; 3 prey ratios made up the other factor.

STRONG PREFERENCE. In the first experiment where the total density of *M. californianus* and *M. edulis* was held constant, no switch occurred and the observed results (Table 8) are consistent with those expected on the basis of equation (2). The preference constant (c), measured by regression as described in the theory section, was 3.6 in favor of *M. edulis.* This preference was the smallest found in any of the "strong preference" experiments. This was also the only strong preference experiment in which the regression estimate of c differed markedly from preference as measured by the ratio eaten in the central treatment ($c = 5.7$). If this latter value of c had been used to calculate the expected percentages in the diet, there would have been a slight suggestion of switching since the treatment with fewer *M. edulis* presented would have had fewer *M. edulis* in the diet (44%) than expected (52%). It is interesting to note also that this experiment, where preference was not very strong, was the only "strong preference" experiment in which large variability among replicates occurred (in the low *M. edulis* treatment in Table 8). However, when the original ratios of the numbers eaten in this treatment were analyzed by χ^2, the heterogeneity among replicates was not significant ($\chi^2 = 5.28$ with 4 d.f., giving $0.2 < P < 0.3$). In addition, when the replicates were then pooled, the observed ratio eaten was not significantly different from expected ($\chi^2 = 1.81$, $0.1 < P < 0.2$), using $c = 5.7$ to calculate the expected ratio. This possible relationship between weak preference and variability is dealt with in much more detail in the next section.

Table 9 shows that in experiment 2, when the two prey were *M. californianus* and *Septifer* and total density was constant, no switch occurred and the results were consistent with the simple model. Deviation from expected appeared to be slightly in the opposite direction from switching. The preference constant as estimated by regression was $c = 0.04$ for *Septifer* ($c = 25.0$ for *M. californianus*). The percentages of *Septifer* were transformed to $2 \text{ arc sin } \sqrt{x}$ for a two-way analysis of variance. Prey ratios offered had a significant effect ($F = 12.90$, $P < 0.001$) but predator size did not ($F = 0.85$).

TABLE 9. (Experiment 2 in Table 7). The expected and observed percentages of *Septifer* in the diet of groups of *Thais* which were given various ratios of *Septifer: M. californianus* for 3 weeks. The calculation of the expected values is explained in the theory section. Each observed value is the mean of 6 observations (three replicates in each of 2 size classes of *Thais* lumped).

% *Septifer* given.............	10	50	90
% *Septifer* expected..........	0.4	3.6	25 0
% *Septifer* observed..........	2.8	7.8	24.8
Range.......................	0–6	0–21	11–45
Total no. prey eaten...........	125	115	67

Fig. 2 shows that in experiment 3, when the

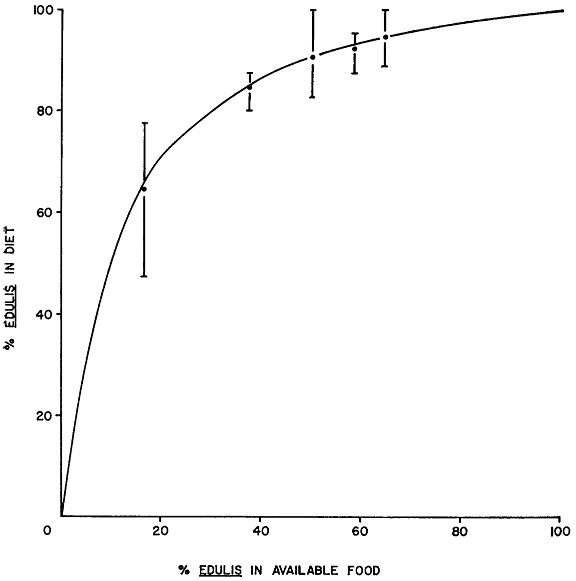

FIG. 2. (Experiment 3 in Table 7.) The means and ranges (vertical lines) of the observed percentage of *M. edulis* in the diets of groups of *Thais* (given *M. edulis* and *M. californianus*). The curve, $Y = 100\ cX/(100 - X + cX)$ where X is the percentage of *edulis* available, shows the expected percentages based on the model of no switching; $c = 9.5$ (see text).

prey ratio offered was changed by holding *M. californianus* density constant and varying *M. edulis* numbers, no switch occurred and the fit to the model was good, with c for *M. edulis* calculated by regression, taking the value 9.5. In all three experiments variability among replicates was rather low, with the one exception in Table 8 already noted.

WEAK PREFERENCE. It has already been established that overall preference between *Balanus* and *M. edulis* was weak in *Acanthina* and that individuals and groups of these snails were easily trained to either prey species. The discussion in the Appendix predicts that when initial preference is weak and when the ratio of *Balanus: M. edulis* is varied, switching and reduced heterogeneity should occur at extreme ratios. However, this expectation was not fulfilled when a switching experiment (number 4 in Table 7) was done using *Acanthina* feeding on *M. edulis* and *Balanus* (Fig. 3). As measured by the diet in the central treatment, $c = 1.1$. Clearly the data do not agree with the model outlined in the theory section (cf. Fig. 2). Very similar results were obtained in experiment 5, not reported in detail, done in cages on the seashore, using *Acanthina* in one set of treatments and *Thais* in another. Preference overall was weak, no switch occurred and heterogeneity was marked.

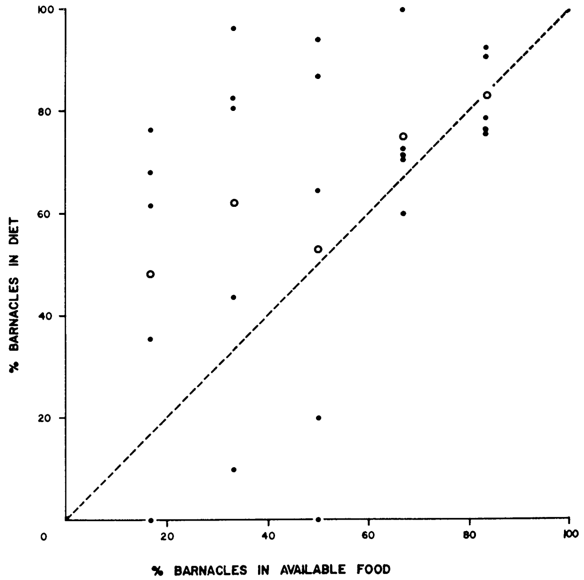

FIG. 3. (Experiment 4 in Table 7.) The observed and mean percentages of barnacles in the diets of five pairs of *Acanthina* at each of five mixtures of *Balanus* and *M. edulis*. The broken line has slope $c = 1$.

Two possible reasons why switching did not occur in these two experiments are: (1) that training did not occur during the experiments and (2) that it did occur, but fewer snails became trained to the abundant species than were needed to produce a higher proportion of that species in the diet than in the food available. I now examine these possibilities.

(1) An analysis of experiments, through time, provides evidence of training, that is that the diet of each group of snails tended to be similar from week to week. For this analysis I have used the data from the two weak-preference experiments described above. I have also used data from the "control" (untrained) treatments of the next experiment described below (number 6). These latter treatments are essentially the same as in the other two experiments: *Acanthina* were given *M. edulis* and *Balanus* at the ratios 30:6, 18:18 and 6:30. In the analysis (Table 10), for each week each replicate was scored as follows. If the number of mussels eaten exceeded the number of barnacles by two or more the replicate was scored + that week, if the number of barnacles eaten exceeded the number of mussels eaten by two or more it was scored —. If the numbers were equal, if they differed only by one or if less than two prey were eaten, no score was made. The number of runs was then counted. A run is a group of like signs, i.e. a series of weeks (1 or more) with successive like signs, weeks with no score being disregarded. A large number of

TABLE 10. The number of runs of plus-and-minus-signs observed in three experiments, and various possible numbers of runs. The way the runs were counted is explained in the text, as is the difference between actual and theoretical maxima, and the origin of the data.

Experiment No.	Predators	Maximum No. (Theoretical)	Maximum No. (Actual)	Observed No.	Minimum No.
4	*Acanthina* (laboratory)	100	79	29	25
6	*Acanthina* (laboratory, "controls")	90	76	26	18
5a	*Acanthina* (seashore)	45	36	17	15
5b	*Thais* (seashore)	45	35	19	15

runs would indicate that the diet changed frequently. Thus, in a replicate in an experiment which lasted 5 weeks, the theoretical maximum number of runs possible is 5 and the minimum is 1. In an experiment with 3 treatments each with 6 replicates lasting 5 weeks, the theoretical maximum is 90 runs and the minimum is 18. Since there were always some weeks with no scores in an experiment, the actual maximum, that is the total number of pluses and minuses, was always less than the theoretical maximum. It is clear from Table 10 that the observed number of runs was close to the minimum in all experiments, supporting the interpretation that training occurred and was maintained most of the time, with few changes of diet in mid-experiment. Considering the diverse origin of the data and the assumptions which would be required, it seems best not to apply statistics. The analysis is unsatisfactory, but I have not found a better method.

(2) If, as seems likely, training occurred in these experiments, then the experimental set-up did not force enough snails to be trained almost exclusively to the abundant prey at extreme ratios. That might follow quite simply from the physical conditions; the prey occurred over a surface area of only 450 cm^2. As I noted in Methods, when the snails were placed in containers with prey, they might spend several hours moving around "handling" the prey before settling down, attacking and eating one prey. Thus they must have encountered individuals of both prey species early on because the rarer prey was fairly common in absolute terms. So training occurred, but the small homogeneous universe did not produce the gradual increase in the probability of attack upon the common species which I outline in the Appendix.

In contrast with the above experiments where no switch occurred, prey populations in nature are distributed over large areas and their distribution can be very patchy. Such a situation might provide exactly the elements, missing in the last two experiments, which would result in switching. The next experiment (number 6 in Table 7) was an attempt to model these features. The situation I envisage is this: the two prey species are intermixed over some parts of the area in which they occur, but the abundant species exists in some spots in essentially pure clumps. These clumps are large with respect to the short term movements of a predator, so that a predator, on encountering such a patch, often might eat several meals there before leaving it. The predator thus becomes trained to the abundant species, and chooses it when it again faces both prey species. A second point is that in nature much more extreme differences in abundance between the two prey are likely than the small range of differences (5:1 to 1:5) which I employed, and a really large difference in prey densities could result in this effect of almost pure patches of the abundant prey.

TABLE 11. (Experiment 6 in Table 7) The numbers of mussels and barnacles attacked over 5 weeks by pairs of *Acanthina* in a factorial experiment with 9 treatments and 6 replicates per treatment. The number of each treatment is in parenthesis at the top of each set of data (see text).

Ratio Mussels/Barracles Given per Week	Trained to Barnacles		Control		Trained to Mussels	
	Mussels	Barnacles	Mussles	Barnacles	Mussels	Barnacles
6M : 30B	(1)		(2)		(3)	
	0	34	22	7	14	5
	3	26	3	29	18	8
	1	25	3	32	26	3
	0	24	6	30	22	3
	0	23	0	40	23	4
	5	16	2	18	22	3
18M : 18B	(4)		(5)		(6)	
	3	24	16	13	32	0
	4	15	4	32	26	3
	5	23	18	10	25	3
	3	16	15	8	29	1
	0	16	24	5	32	2
	3	36	21	5	24	3
30M : 6B	(7)		(8)		(9)	
	11	11	16	9	25	0
	2	20	25	1	25	0
	22	6	27	8	38	0
	20	11	19	4	29	0
	11	6	21	6	30	1
	2	12	31	3	24	0

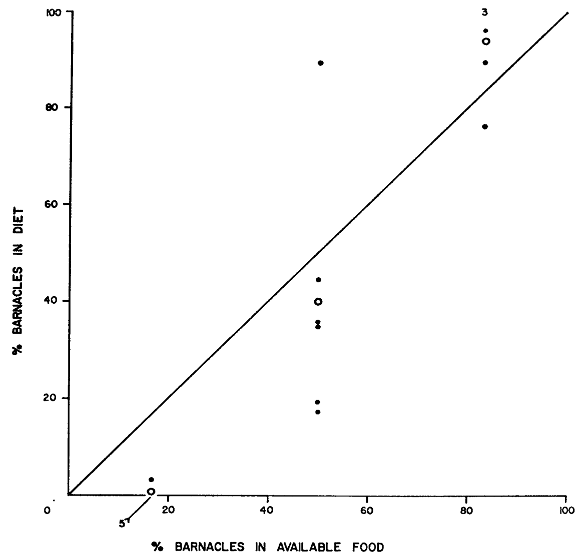

FIG. 4. (Experiment 6 in Table 7.) The observed and mean percentages of barnacles in the diets of 6 pairs of *Acanthina* in each of 3 treatments. The snails given 16.7% barnacles were trained to mussels, those given 50% barnacles were untrained and those given 83.3% barnacles were trained to barnacles. Five replicates ate 0% barnacles and 3 replicates ate 100% barnacles. The line has slope c = 1.

The next experiment (Table 11) tried to incorporate the patchiness of the prey species, but in time rather than space. Groups of *Acanthina* were fed for 4 weeks only *M. edulis* (mussel), only *Balanus* (barnacle), or nothing at all (control). The experiment was factorial, the other factor being the three different prey ratios given after the training regimen.

The results from three treatments (numbers 1, 5 and 9 in Table 11) are graphed in Fig. 4. The question asked here is, do the snails switch when they have had a chance to become trained to the abundant prey species? Obviously switching should also be accompanied by reduced heterogeneity at the extreme prey ratios. Switching occurred. The 2 treatments (4 and 6) in which trained snails were given equal numbers of the two prey species might also be considered as a test of the idea. These treatments model the situation where the two prey species have unequal abundances; outside the pure clumps of the more abundant prey (modelled by the training period), the two species are equally abundant. Switching occurred by this test also, since snails trained to barnacles ate 88% barnacles during the test period, while those trained to mussels ate 93% mussels (Tables 4 and 11).

A second point is that, in nature, if a predator has switched to a prey when it is abundant by becoming trained to it, it should become "retrained" and switch to the alternative prey when that species becomes abundant. Treatments 4 and 6 in Table 11 (also Table 4) show that the training effect was strong, even over five weeks, when the prey were equally abundant, so one would expect to find a definite time lag in retraining. On the other hand, within 5 weeks one might find some evidence of retraining if snails which had been trained to one species were presented with a mixture in which the alternative species was more abundant. To get at the changes through time, the percentage of barnacles eaten each week in each treatment was calculated by lumping the data for all replicates. (Each replicate in each week had rather low numbers to treat replicates separately.) These data are in Table 12, where it can be seen that a clear "reverse switch" occurred in treatment 7 where training was to barnacles, but did not occur in treatment 3 where previous training was to mussels. Thus, this point is not answered clearly in the experiment. An examination of Tables 11 and 12 may indicate why there was no reverse switch to barnacles when these were abundant. First, from Table 11 it can be seen that there was an over-all pref-

TABLE 12. The percentage of barnacles in the diets of snails in nine treatments over 5 weeks. The treatment numbers correspond with those in Table 11.

Treatment No.	Treatments		Week				
	Feeding Regimen	Prey Ratio Offered	1	2	3	4	5
1	Barnacles	6M : 30B	97.8	95.0	93.8	90.3	93.3
2	none	6M : 30B	82.4	89.2	82.9	77.8	67.9
3	Mussels	6M : 30B	25.0	9.1	10.7	29.4	10.7
4	Barnacles	18M : 18B	97.5	100	96.8	81.5	62.1
5	none	18M : 18B	39.5	66.7	40.7	32.1	25.8
6	Mussels	18M : 18B	10.0	12.5	3.4	2.8	0.0
7	Barnacles	30M : 6B	81.3	59.3	47.8	36 4	13.8
8	none	30M : 6B	17.9	34.0	16.7	11.1	0.0
9	Mussels	30M : 6B	2.1	0 0	0.0	0.0	0.0

erence for mussels, and this is reflected in the central control treatment (5). Secondly, from Table 12, it appears that there was a rather general pattern in the data. In 5 treatments (numbers 2, 4, 5, 6 and 8) there was an increase in the percentage of barnacles eaten in the second week, then a gradual decline over the last 3 weeks. This suggests that the quality of the prey changed during the experiment (from week 3 onwards barnacles were taken from a patch adjacent to the area from which they were taken during the first two weeks). The four treatments which did not fit the pattern are as follows: (a) treatment 7 where a clear switch to mussels was evident throughout the experiment; (b) treatments 1 and 9 where the snails were trained to a species which was then made very abundant. Here the percentages were extreme and rather constant through time, as one might expect. (c) Finally, the other expected reverse switch, treatment 3, showed irregular changes in percentages. The data suggest, then, that a fairly weak but quite definite increase in preference for mussels from week 3 onward prevented any tendency for a reverse switch to barnacles in treatment 3, and further support the notion that symmetrical switching is likely to occur only when preference is very slight.

In summary, the experiment clearly demonstrated switching following training, but the evidence for a reverse switching over the 5 weeks is not clear-cut, probably owing to a qualitative change in the prey.

Functional Response

The functional response is the way in which the number of prey eaten per predator (over a short period) changes with prey density. Although the major purpose of this work was not to study the snails' functional response *per se,* some of the data presented in the experiments already described bear on this problem as do some other experiments not reported so far. In this section I examine the response in two main situations: (a) one prey species present and (b) two prey species present, and in three types of circumstances in the latter situation: (i) where preference was strong, (ii) where it was weak and no switch occurred and (iii) where a switch occurred.

Holling (1959) has distinguished three types of functional response. In type 1 the number of prey eaten rises linearly to a maximum. In type 2 ("invertebrate"), as prey density increases the number of prey eaten per predator also increases, but at a decreasing rate, so that a maximum value is reached or approached. This produces a decreasing percentage mortality on the prey as its density increases. In type 3 ("vertebrate"), as prey density increases, the number eaten forms a sigmoid approach to a maximum, the rate of increase at first accelerating then decreasing. This type produces initially increasing percentage mortality on the prey then declining percentage mortality.

I had three questions in mind in this section. The first was whether or not the predators showed the typical "invertebrate" response to increasing prey density when one prey species was present. The second question was whether this type of response changed when two prey species were present. The third question was whether, under some circumstances, the response changed to one in which the number of prey eaten increased at an increasing rate, over at least part of the density range, giving either a continually accelerating curve or a sigmoid curve (type 3).

The functional response experiments were designed as follows. Snails in different treatments were presented with different densities of one prey species and, as usual, all prey were replaced each week. The functional response should relate number attacked to number present, but of course during any week the prey density gradually declined, and the relationship measured is number eaten versus initial number in each week. Clearly the error is relatively great at low densities. I consider this change in numbers relatively unimportant since I did not try to estimate the parameters of the function but merely tried to discover the general form of the curve. In most studies reported to date prey have not been replaced as they were eaten, though Holling's (1965) experiments with mantids are an exception. All experiments involving two prey species have been described in previous sections.

SINGLE PREY SPECIES. For various reasons, predator density was not the same in all experiments, and the effects of predator density and prey density were measured (Table 13). Prey, but not predator, density had a significant effect ($F = 8.8$, $P < 0.025$) on the number eaten per snail. Connell (pers. comm.) has unpublished data showing that solitary *Thais canaliculata* eat more barnacles per snail than do pairs of snails. The data for two other species of *Thais* show no significant difference between solitary and paired snails. Thus, there may be a depressing effect of predator density at low densities only.

The next experiment examined the relationship in *Thais* between predation rate and prey numbers (*M. edulis*) (Fig. 5). The percentage of the

Table 13. The total number of *M. edulis* per replicate attacked by groups of *Thais* over 5 weeks.

No. of *Thias*	No. of Mussels Offered	
	10	20
5	14 21 10 15	30 29 12 29
10	27 37 34 34	40 43 42 47

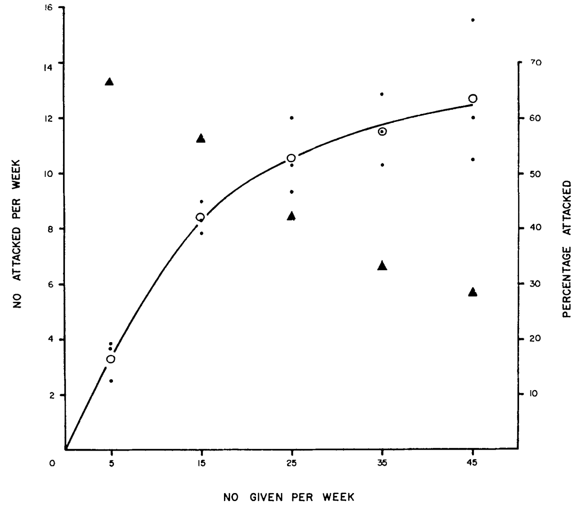

Fig. 5. The number of mussels and the mean number of mussels attacked per week, and the mean percentage attacked (black triangles) of those available are graphed for three groups of 10 *Thais* at each of five *M. edulis* densities. The experiment ran for six weeks. The curve was fitted by eye.

prey eaten declined with prey density, as in all responses of this sort (type 2), so that such a functional response, on its own, would not cause stabilizing prey mortality. Variability among replicates was rather low.

Fig. 6 shows the response in groups of *Acanthina* which were given different densities of the mussel *M. edulis*. The general form of the functional response in *Acanthina* was also "invertebrate," though the response seems weaker at higher densities than it was in *Thais*. As in the previous experiment, replicates were not very variable.

The conformity of these results with other data on invertebrates (Holling, 1965) is more surprising than it may seem, for the other predators studied had to hunt for their prey and the rising response curves can be explained on the basis of increasing numbers of contacts with prey. When hunting is unimportant a horizontal line might be expected.

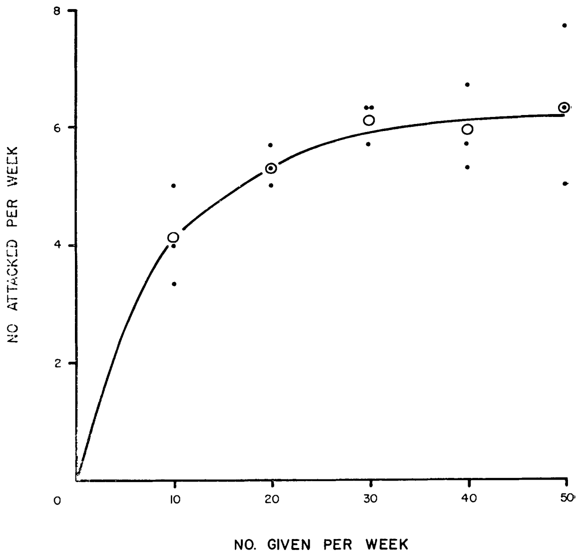

Fig. 6. The number of mussels and the mean number of mussels attacked per week by 3 groups of 5 *Acanthina* at each of 5 *M. edulis* densities. The experiment ran for 3 weeks. The curve was fitted by eye.

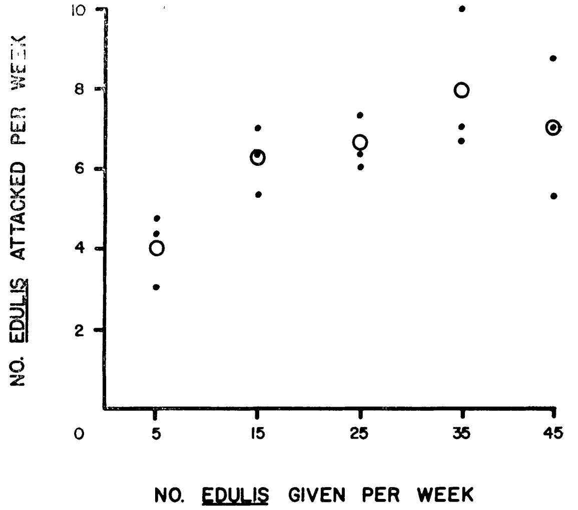

Fig. 7. The number of mussels and the mean of mussels attacked per week by groups of 10 *Thais*. There were 5–45 *edulis* and 25 *californianus* in each box. The experiment lasted 3 weeks.

two prey species. The data presented in this section come from experiments described already. These experiments were designed to answer questions about switching, but they yield information about the change in number of prey eaten with the number given (I will continue to call this a "response"). However this was not the main purpose of these experiments and there are too

TABLE 14. The percentage of the preferred prey which was attacked in 2 experiments in which groups of *Thais* were presented with varying ratios of 2 mussel species with total prey density constant.

A. Pairs of *Thais* attacking *M. edulis* and *M. californianus*. Prey density 36, experiment lasted 5 weeks, 5 replicates.

No. *M. edulis* given	6	18	30
Mean (and range) percentage attacked	25.3 (13-40)	15.3 (8-23)	14.7 (11-17)

B. Small and large *Thais* attacking *Septifer* and *M. californianus*. Prey density 100, predator density 20, experiment lasted 3 weeks, 3 replicates.

No. *M. californianus* given	10	50	90
Mean (and range) percentage attacked by large *Thais*	49.7 (43-53)	15.7 (15-17)	11.7 (11-13)
Mean (and range) percentage attacked by small *Thais*	30.0 (20-37)	12.7 (11-16)	7.7 (7-8)

few treatments to allow an adequate analysis of the response.

(i) Preference strong. Fig. 7 shows the number of *M. edulis* eaten when *Thais* were presented *M. edulis* ranging from 5 to 45 per container, together with 25 *M. californianus*. The same range of *M. edulis* was given in the functional response experiment described above. The form of the response was similar in both experiments (cf. Fig. 5 and 7). The number attacked declined at the highest density in Fig. 7, possibly because the boxes were by then rather crowded. Table 14 shows that, as in the typical "invertebrate" response noted above, the percentage attacked again declined as density increased in the other two strong-preference experiments where *Thais* had to choose between two mussel species. Variability among replicates was rather low in all three experiments.

(ii) Preference weak—no switch. Fig. 8 graphs the numbers of mussels and barnacles eaten in the major weak-preference experiment. The means for barnacles may approximate the usual response curve; the approximation is worse in the mussels. However, for both prey species individual replicates regularly lie far from their mean values, in sharp contrast to the strong preference experiments described above. The regular type 2 response of Holling is a poor description of these data. Other, similar, data are in Table 11, treatments 2, 5 and 8.

(iii) Preference weak—a switch occurred. When switching occurs it is possible, but not guaranteed, that the mortality caused to the prey will be stabilizing, that is, that the curve of numbers eaten versus numbers given will be either continually accelerating or sigmoid, thus giving an increasing percentage mortality over all or part of the range of prey density.

The data from the three relevant treatments (1, 5 and 9, Table 11) of the switching experiment which incorporated training are graphed in Fig. 9. There was reduced variability among replicates at the low and high densities. The mean percentages attacked were:

No. prey given per replicate in 5 weeks	30	90	150
% of barnacles attacked	0.5%	13.6%	16.5%
% of mussels attacked	5.0%	18.1%	19.0%

Two conclusions can be drawn. First, the response to prey density again was not the typical one found previously in invertebrates. Second, prey mortality was density dependent and thus potentially stabilizing over the lower density range. There is a suggestion that the percentage eaten levelled off at the highest density.

DISCUSSION

This study was designed to see if, under laboratory conditions, predatory snails switch (as defined in Theory) from one prey to another as prey abundances change. In the mechanism suggested by Elton (1927, *loc. cit.*) and discussed in the Introduction, switching is a necessary, though not a sufficient condition for general predators to cause stabilizing mortality on prey populations.

The first conclusion is that no switch occurred under most circumstances. This conclusion held where preference was either strong or weak, except in some particular circumstances. The second conclusion defines these circumstances as follows: if the predator had a weak preference for one of two prey species, and it had a chance to become trained to whichever prey was abundant, it switched. A patchy prey distribution might provide this opportunity in nature. Clearly, this mechanism may work in nature, but this depends in part upon how strong preferences are in general. Patchy prey distributions probably are the rule, but presumably only some kinds of patchy distributions would lead to training. In particular, the right kind of distribution would produce patches of prey which were large relative to the

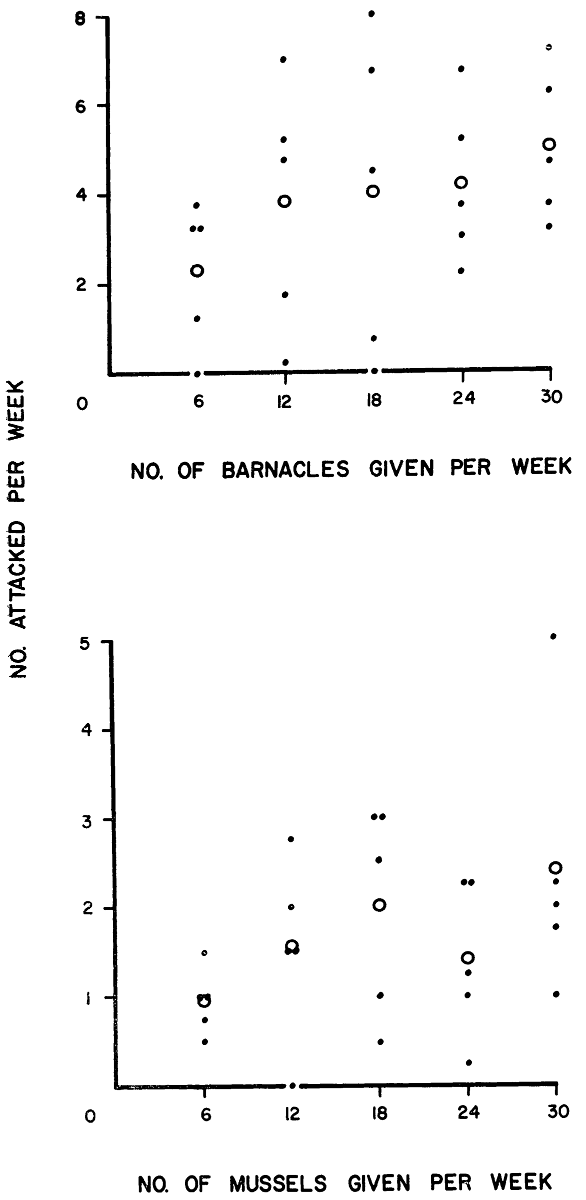

FIG. 8. (Experiment 4 in Table 7.) The number and mean number of prey attacked per week by 5 pairs of *Acanthina* at each of 5 mixtures of barnacles and mussels.

area searched by a predator in the course of obtaining several consecutive meals.

When preference was strong the ratio of the two prey in the diet appeared to fit a simple model of predation (Theory) in which the predicted ratio in the diet is proportional to the ratio given.

One possible interpretation of the general absence of switching in the systems used here is that the snails and/or their prey possess peculiar characteristics not found generally in predator-prey systems. I will mention three possibilities. First, conceivably, in nature the snails have not faced conditions favoring the evolution of switch-

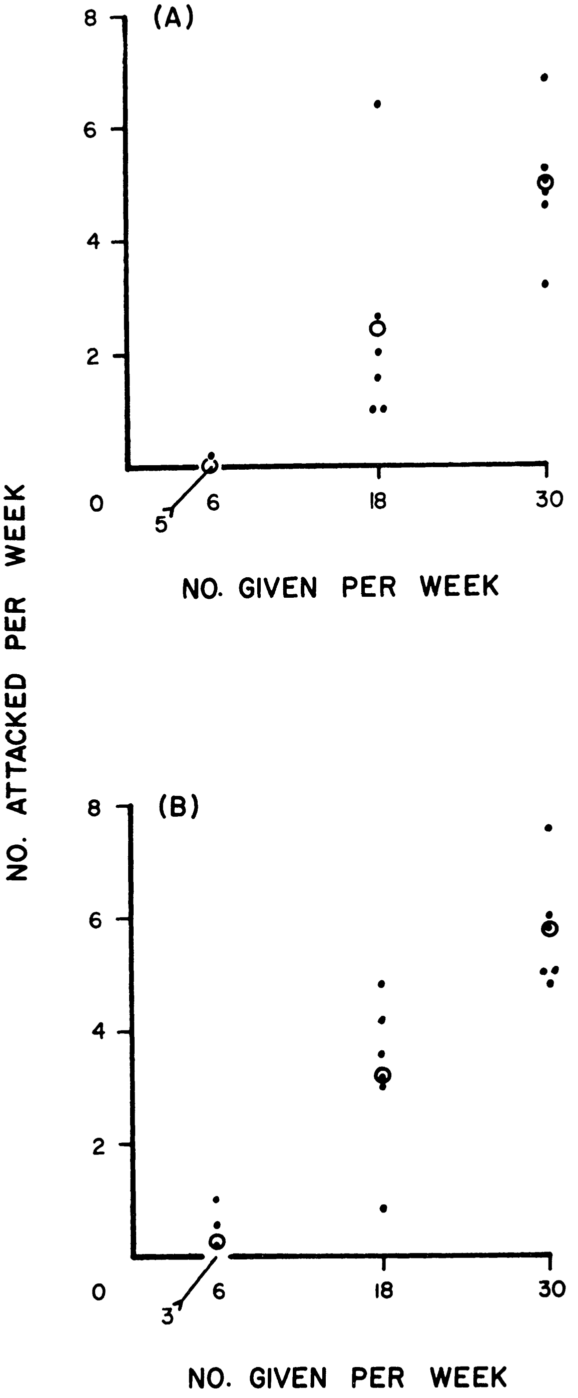

FIG. 9. (Experiment 6 in Table 7.) The number and mean number of prey attacked per week by 6 pairs of *Acanthina* in each of 3 treatments; (A) attacking barnacles, (B) attacking mussels. Snails given 6 barnacles: 30 mussels were trained to mussels, those given 18 of each were untrained, those given 30 barnacles: 6 mussels were trained to barnacles. Notice that 5 and 3 replicates attacked none of the rare prey.

ing behavior. Certainly, in a sense they cannot stabilize their prey populations, since the prey have planktonic larvae; however it is not clear that this fact is relevant to the question of the evolution of switching behavior. Indeed, it would be interesting to try to distinguish those circumstances under which switching should evolve. Second, the behavior of the prey is unusual in that, in essence, they don't move, while the predators showed little evidence, in the experimental conditions used here, of complex searching behavior. The predators appeared to blunder into the prey; I could see no evidence that they detected them or were attracted to them from a distance. Yet the predators almost never attacked the first prey they touched, they examined many prey, and it may be that a complex choice was made among those individuals of a species which were touched; for example, the predators have a size preference. Connell (pers. comm.) has the idea that they may be searching for individuals which are in some way more vulnerable to attack. Wood (1968) has shown that predatory snails can follow prey fluids in the laboratory. The best approach to the question of whether or not the system is peculiar is to test the conclusions in other systems. In particular it would be interesting to look at predators which clearly have a complex searching behavior (such as insect parasites and some vertebrates), especially if the searching behavior were different for different prey species and if the prey individuals were spaced out or hidden so that contacts with prey were rather infrequent. A third possibility is that the absence of switching was merely an artifact of the simplifications of the laboratory, and indeed I have suggested that heterogeneity should produce switching in some circumstances. While my experimental system clearly was artificial (in general that is the reason for working in the lab), in nature the snails frequently are in rather similar situations in which they are surrounded by readily available prey of one or a few species, for example, in mussel clumps. Further, their strong preference between mussel species seems to be carried out into the field (Harger, 1967). The one experiment I did in cages on the seashore gave results similar to those obtained in the lab. Again, the best way to answer the question is to try to find a suitable test in the field.

Since the experiments described here were completed, Wood's (1968) study on the predatory snail *Urosalpinx* has been published. He sampled snails feeding on mussels and barnacles on the sea-shore and tried to estimate the densities of each of these prey on the shore close to the snails. His tentative conclusion was that the ratio of the numbers of attacks on the two kinds of prey equalled the ratio of the numbers of the two kinds present locally. This suggests that no switching was occurring, though Wood cautions that his estimates of prey densities were not very reliable; in addition the past history of prey densities and predator attacks was not known.

I now turn to the conclusions concerning the number of prey eaten at different prey densities. The snails, given a range of densities of a single prey species, showed the typical type 2 functional response which has been demonstrated in many other invertebrate predators and in parasitoids (Burnett, 1951 & 1954; Holling, 1965), though it is not present in all the parasitoids studied (Burnett, 1964; Takahashi, 1968). In this response the percentage predation declines with increasing prey density. When two prey species were present and preference was strong, the percentage mortality of one prey species still declined with increasing density of that species, both when total prey density was constant and when it varied. When preference was weak and no switch occurred, there was a great deal of heterogeneity among replicates and no clear statement could be made about the relationship between prey density and predation rate. When switching occurred and total prey density was constant, mortality in each prey species was density dependent, at least over the lower range of prey densities. This is Holling's type 3 predation. Clearly then, from a knowledge of the functional response when one prey species is present, we cannot always predict how the number of prey eaten will change with the number given when two species are present and preference is weak. Finally, switching is potentially a stabilizing mechanism, though whether it would have this effect when total prey density varied, or in nature, is another matter.

These conclusions about switching and functional response, derived from snails under artificial conditions, should be regarded as predictions. It is of interest to see if they hold in other organisms and in nature, and they could be tested by studying metazoan invertebrate predators (including insect parasitoids) which hunt in some fashion. Landenberger (1968) showed that starfish show little preference between two prey, *Tegula* and *Acanthina*. When the prey ratios were varied and total prey density kept constant, the proportion of one species in the diet was equal to the proportion given. Thus there was no switch. He also noted some heterogeneity among replicates, though it was generally not as great as that found in the analogous situation in this study. His results are consistent with the conclusions I noted above.

There is suggestive evidence that vertebrates differ from invertebrates in their response to changes in the *relative* abundance of their various prey species (Holling, 1959 & 1965; Tinbergen, 1960). Unfortunately, the field data in these papers are not directly comparable with the criterion for switching, since predation rates (Holling) or the percentage of one species in the diet (Tinbergen) are compared with the absolute density of one prey species in the environment. The data, of course, were not collected with switching in mind, though Tinbergen's "search image" idea is similar. Also, it is not clear that Tinbergen's data in fact provide evidence of a sigmoid relationship between prey density and percent prey in the diet. Holling (1965) has pointed out that it seems unlikely that a vertebrate-invertebrate classification of predatory behavior would hold in general.

The conclusions I have outlined apply to the particular switching mechanism I have examined which hypothesizes changes in the predators' behavior. There are several other mechanisms which might produce the kind of change in the diet required by the definition of switching outlined in the Theory Section. Thus as I noted in that section, prey behavior, which changes the prey's availability, might influence the ratio of prey in the diet at different relative prey densities. I have not examined this possibility. In the next few paragraphs I examine some other possibilities.

Predators might "switch" to a prey species only at relative abundances more extreme than I have examined. As I noted in the Theory Section, I have restricted my use of the term switching to changes in the diet which occur around a prey ratio of unity (Fig. 1). Obviously, one has to set some limits to the range of ratios within which a change in diet will be accepted as switching, otherwise there is no way of disproving the null hypothesis of no switching.

Another possibility is that switching might occur over longer time periods than I have considered. For example, predators might become imprinted to whichever prey is abundant when the predators are young (Thorpe, 1939; Thorpe & Jones, 1937). Or, again, there might be a genetic polymorphism among predators with respect to prey preference or ability to handle particular prey species. Then different predator genotypes might increase at different rates according to the abundance of different prey species. Clearly both mechanisms would involve time lags in the predators' response to changes in the composition of the available prey; these lags would be longer than the lag in the behavioral mechanism I have been studying. Such lags ought to lead to oscillations in prey numbers rather than stability. These two possibilities seem unlikely in the snails in the light of the experiments described here.

The kind of changes in diet examined have occurred in the same place. Some predators probably do vary their diet, in a fashion akin to switching, when large-scale population movements are taken into account. For example, large predatory birds in the Arctic may converge from widely separated areas to attack lemmings when these prey reach peak numbers (Pitelka *et al.*, 1955). Usually lemmings may form only a small part of the birds' diets. Again, this kind of predatory behavior is quite different from what I have been considering here and from the notion of switching found in the literature. This large-scale movement of predators seems to be characteristic of unstable systems.

I shall now indicate briefly two rather general areas where this study has some relevance. First, if the conclusions are generally applicable, then the problem of whether or not invertebrate predators can stabilize their prey is rather more complex than might have been expected. The predators' capacity to do this, of course, will depend on all the components of the predator population's response, numerical as well as functional. But given that these other components have been measured, it is not enough to know the form of the functional response to the prey species in question alone. The number eaten will be influenced by the degree of preference the predator has for alternative prey species, by the predators' opportunities for becoming trained to various prey species, and by the way the densities of other prey are changing. (The total response also will depend on the predators' rate of increase and movements, etc., but these are additional problems to those raised here.) It seems possible that a general predator might have a stabilizing influence on some subset of its prey species, among which its preferences are weak, but not on the remaining species in its diet.

A possible conclusion from the results, if they are generally applicable, is that switching in nature probably is rare, and that at least invertebrate predators in general do not stabilize the numbers of their prey by this mechanism. This is not to say that invertebrate predators do not produce stability or sometimes limit the numbers of their prey. Evans and Murdoch (1968) have noted that in an insect community the average herbivore species is attacked by very many species of predators and parasites, and it may be that the combined effects of these predators, rather than the effect of any one predator species, limit many herbivore populations.

The other major area where this study has some relevance is in competition between prey species and the influence which competition has upon species diversity. One obvious possible consequence of switching in a predator feeding on two potentially competing prey species is that the two prey might be able to co-exist indefinitely owing to heavy predation on whichever species was winning in competition. At least within wide limits, an increase in predation may cause an increase in prey species diversity, both in numbers of species and in the evenness of their relative abundances (Connell and Orias, 1964; Paine, 1966). Features such as the presence or absence of switching and the form of the functional response probably will have a large influence on whether or not increased predation will lead to increased prey diversity. General predators which switch are likely to increase diversity, those which don't switch should increase prey diversity mainly if they prefer prey which tend to win in competition. An adequate analysis of such predictions, though, requires information on the total predator responses which come about when different types of individual predatory behavior are integrated with other aspects of predation. Except for the work of Holling (1959) this has not yet been attempted.

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APPENDIX: TRAINING AND SWITCHING

Here I examine the consequences of training only for the situation where preference is weak. If a predator is presented with two prey species, I conclude that training has occurred when the probability that the predator will eat one of the species is increased by feeding it that species before it chooses between the two prey. When the ratio of the two prey varies, training should then lead to switching as follows. Consider a group of predators which have had no previous experience with and have no preference between the two prey they are presented with. Let the proportion that prey species 1 forms of the food available be p. Assuming that the probability of encounter for each prey species varies with the abundance of the species (i.e., they are equally "available"), then the probability that the first meal of a predator will be species 1 is p, and proportion of predators (P_1) whose first meal was species 1 is p.

Then, before the second meal, a proportion p of the predators have a slight preference for species 1, and $(1 - p)$ have a slight preference for species 2. Let the training effect of eating one prey individual be α. Then a predator which has eaten one prey individual of species 1 will now eat species 1 on its second meal with probability $p + \alpha$. Similarly, a predator which has eaten species 2 on its first meal will now eat species 1 with probability $p - \alpha$. Thereafter, any given predator has either probability $p + \alpha$ or $p - \alpha$ of eating species 1, depending on its last meal. Switching occurs when there is an increase in the proportion of predators in one of these two states.

Thus the proportion of predators which eat species 1 on the second meal (P_2) is $p(p + \alpha) + (1 - p)\ (p - \alpha) = p + \alpha\ (2p - 1)$. When $p > 0.5$, $\alpha\ (2p - 1) > 0$, and by the second meal species 1 will form a higher proportion of the diet of the group of predators than it does of the food available if species 1 is the more abundant species. Similarly, if species 1 were the less common species, $2p < 1$ so that $\alpha\ (2p - 1) < 0$, and species 1 would form a smaller proportion of the diet than of the food available. (Clearly where $p = 0.5$, species 1 forms ½ the diet of the group of predators.) Thus switching occurs by the second meal. In general for the $n + 1$ meal, $P_{n+1} = p + \alpha\ (2P_n - 1)$ and the degree of switching, P_n, increases asymptotically to $P_{max} (P_{max} < (p + \alpha) < 1)$.

In this model the predator "remembers" only its most recent meal, and the training and switching effects are minimal. It seems likely, however, that a predator which has eaten several meals of species 1 would be more trained to that species than an individual which has eaten only 1 meal. When this is the case, the probability that a given predator will eat species 1 can exceed $p + \alpha$ (but must be less than 1). Presumably the training effect of a meal, initially α, would decay as subsequent meals are eaten, and I have examined the consequences of several assumptions of this sort. For example I assumed that the training effect of a meal decays geometrically. When this sort of assumption is made, not only can each predator become trained to a greater degree, but switching occurs faster and becomes more extreme than in the simpler case discussed above. I have no data on which to make assumptions about either the relationship between the number of meals eaten of a given species and the degree of training, or between the order of meals in a mixed diet and their subsequent training effect.