

## Variable Predators and Switching Behavior

PETER L. CHESSON

*Department of Zoology, The Ohio State University,  
1735 Neil Avenue, Columbus, Ohio 43210*

Received June 29, 1979

Models are developed in which prey preferences vary between individual predators but the preference of an individual does not change with prey relative density. These two properties generally lead to the surprising conclusion that the aggregate preference of a population of predators does change with prey relative density. This phenomenon may result in negative or positive switching, depending on the circumstances, with negative switching being the more likely result. Such population negative switching is found in previously published experimental data. Implications are given for the analysis of ecological data, and some implications for the stability of field populations are suggested.

### 1. INTRODUCTION

Murdoch (1969) introduced the term "switching" to refer to the situation where the ratio of the abundances of two prey species, in the diet of a predator, increases faster than proportionately with their ratio in the environment. Murdoch believed that switching (to be called here "positive switching") would stabilize prey species densities, and theoretical evidence for this was found later (Oaten and Murdoch, 1975; Tansky, 1978).

P. L. Chesson (1978) introduced the term antiswitching (to be called here "negative switching") to describe the situation where the ratio of two prey species in the diet of a predator increases slower than proportionately with their ratio in the environment. Switching behavior, i.e., the presence of either positive or negative switching, is usually thought of as a behavioral phenomenon involving predator individuals: individual predators change their preferences for the prey species as prey relative densities vary. A variety of mechanisms by which individuals may show positive switching has been worked out theoretically (Murdoch and Oaten, 1975; Oaten and Murdoch, 1975; Murdoch, 1977; McNair, 1980). However, the interesting effects of switching behavior occur at the population level: the predator population as a whole influences the stability of the prey populations. To obtain the effect of the entire population of predators one must sum the effects of each individual. This is a simple matter if individuals are identical

in all respects, for then the effect of the predator population is a direct reflection of the behavior of an individual. However, if individuals are not identical, summing the effects of the individuals can be quite complicated, and as we shall see, the qualitative effects of the entire predator population may not be predictable from the qualitative behaviors of the individuals making up the population.

In this paper models are introduced where *individual* predators show no switching behavior, yet at the population level switching behaviour occurs. The predator individuals in these models differ from one another in prey preference, in prey handling time, and in other ways. Thus the predators show between-individual variation (P. L. Chesson, 1978). It is to be expected that some between-individual variation will be found in almost any quantitative aspect of behavior. For prey preferences, this between-individual variation can be quite extreme (Murdoch and Oaten, 1975), and it is shown here that between-individual variation can cause both positive and negative switching for the population of predator individuals considered as a unit. A reanalysis of experimental data of Murdoch (1969) gives empirical support to these theoretical ideas.

The intuitive essence of the findings below can be explained in terms of a partial decoupling of the effects of the predator population on the two prey populations, as a result of between-individual variation. This is most easily seen for the standard type II functional response, which models the effects of handling time and satiation. With this functional response, an increase in prey density results in a decrease in the per capita predation rate, i.e., a decrease in the number of prey eaten per unit time divided by the number of prey individuals. Handling time and satiation affect a predator individual's predation rates for both prey species, indeed handling time and satiation change the per capita predation rates proportionately for the two species. For instance, if one prey species increases in abundance, while the other remains constant, the per capita predation rates for the two species decrease by proportional amounts due to an increase in total handling time, or the level of satiation. Thus in the presence of just one predator individual, or a population of identical predators, there is a very close coupling of the per capita predation rates for the two prey species.

The presence of variation in preference for the prey, from one predator individual to another, leads to a partial decoupling of the per capita predation rates. For instance some predator individuals may have a high preference for species 1, and these predators may therefore have little effect on species 2, while other predator individuals have a high preference for species 2 and little effect on species 1. In this situation, if species 1 increases, and species 2 decreases, the per capita predation rate on species 1 decreases, while that on species 2 increases. Thus in the diet of the predator population as a whole, the ratio of the two prey species varies inversely with their ratio

in the environment, i.e., negative switching occurs at the population level even though individual predators show no switching behavior.

Population negative switching effects are given a rigorous general treatment below. It also shown that positive switching can result at the population level, under certain circumstances, e.g., if the functional responses are type III, i.e., accelerating functional responses.

These population level phenomena provide a new view of the relationship between collective and individual behavior. In different circumstances the focus can be on phenomena that occur at the individual level, or on phenomena at the population level. Distinguishing between these levels poses important methodological and statistical problems, requiring more care in data collection and analysis.

Population level switching behavior has implications for population dynamics. Indeed, as discussed below, a general tendency toward population negative switching might be expected to occur when prey are abundant, leading to the possibility of destabilization of the prey populations.

## 2. MODELS FOR THE BEHAVIOR OF AN INDIVIDUAL

In this section we discuss models for individual predators with no switching behavior. In later sections we show how switching behavior arises for a population of predators with individuals behaving according to the models presented here, but with the model parameters varying between individuals.

Let the two prey species have densities  $H_1$  and  $H_2$  and let  $X_1$  and  $X_2$  be the mean rates of consumption of these two prey species by a particular predator individual. Murdoch and Oaten (1975) define (positive) switching in terms of

$$c = (X_1/X_2)/(H_1/H_2).$$

Positive switching occurs if  $c$  is an increasing function of the relative density  $H_1/H_2$  (or equivalently  $H_1/(H_1 + H_2)$ ) of species 1. Conversely, if  $c$  is a decreasing function of relative density we say that negative switching occurs.

Switching behavior can also be defined in terms of preference measures (J. Chesson, 1978) which are related to  $c$  as follows:

$$\text{preference for species 1} = \alpha_1 = c/(1 + c),$$

$$\text{preference for species 2} = \alpha_2 = 1/(1 + c).$$

Since  $\alpha_1 (= 1 - \alpha_2)$  is an increasing function of  $c$ , switching is positive or negative depending on whether  $\alpha_1$  is an increasing or decreasing function of

relative density. These preferences define the proportion of the diet made up by species 1 according to the formula

$$\frac{X_1}{X_1 + X_2} = \frac{cH_1}{cH_1 + H_2} = \frac{\alpha_1 H_1}{\alpha_1 H_1 + \alpha_2 H_2}. \quad (1)$$

At equal prey densities the proportion (1) is equal to the preference.

The mean consumption rates  $X_i$ , as functions of prey densities, are the functional responses and we shall denote them by  $f_i(H_1, H_2)$ . Denoting mean total prey consumption by  $f_T(H_1, H_2) = f_1(H_1, H_2) + f_2(H_1, H_2)$  we find from (1) that

$$f_i(H_1, H_2) = f_T(H_1, H_2) \frac{\alpha_i H_i}{\alpha_1 H_1 + \alpha_2 H_2}. \quad (2)$$

Functional responses that give no individual switching behavior are obtained from (2) simply by assuming that  $\alpha_1$  and  $\alpha_2$  are independent of  $H_1$  and  $H_2$ . The total functional response,  $f_T(H_1, H_2)$ , can be of any functional form, but in general it will depend on  $\alpha_1$  and  $\alpha_2$ .

The simplest functional response giving no individual switching behavior is the linear or type I response where the amount of species  $i$  consumed is simply proportional to the density of species  $i$ :

$$f_i(H_1, H_2) = \rho \alpha_i H_i. \quad (3)$$

In this equation no allowances are made for handling time or any changes in hunting rate due to satiation or hunger, and no allowances are made for possible effects from hunting the other prey simultaneously. The parameter  $\rho$  is an overall hunting rate.

The next simplest functional response is a type II response where the predator does take time to handle prey but otherwise the predator's behavior is no different than in the linear response. This is the two-prey generalization of Holling's disk model (Murdoch and Oaten, 1975):

$$f_i(H_1, H_2) = \frac{\rho \alpha_i H_i}{1 + \rho \{ \alpha_1 \eta_1 H_1 + \alpha_2 \eta_2 H_2 \}}; \quad (4)$$

where  $\eta_i$  is the mean handling time for prey species  $i$  and now  $\rho$  is an overall hunting rate during search time.

The disk model (4) originated as a deterministic model, but it can also be derived as a mean capture rate in stochastic models (Oaten and Murdoch, 1975; McNair, 1980). This is important because Oaten (1977) has shown that stochastic models are necessary for the adequate representation and interpretation of the behavior of an individual animal. Oaten and Mur-

doch (1975) and McNair (1980) actually derive equations more complicated than the disk equation, for in their models they allow for training effects where previous meals influence capture probabilities, handling times, and encounter rates. These training effects lead to individual switching behavior, but when they are removed, mean capture rates corresponding to the disk equation (4) are found.

In cases when total absolute density ( $H_1 + H_2$ ) is large,  $\rho$  is large, or handling times are large, then searching time is small relative to handling time and the disk model (4) reduces to

$$f_i(H_1, H_2) = \frac{\alpha_i H_i}{\alpha_1 \eta_1 H_1 + \alpha_2 \eta_2 H_2} \quad (5)$$

which we shall call the saturated disk model.

In the models presented so far, the predator responds only passively to prey density: it simply eats what is available in the time available. There is no reduction in the hunting rate at high prey densities due to satiation and there are no learning effects at lower prey density that could increase the hunting rate to give a type III response. Such effects can be included by modifying the linear model so that the hunting rate  $\rho$  is a function of prey densities. The hunting rate should change to reflect the total value of prey consumed. If  $v_1$  and  $v_2$  are the values of prey 1 and prey 2, then the total value of prey consumed is proportional to  $\alpha_1 v_1 H_1 + \alpha_2 v_2 H_2$  and the linear response is modified by making  $\rho$  a function,  $\rho = r(z)$ , of  $z = \alpha_1 v_1 H_1 + \alpha_2 v_2 H_2$ . When  $r$  is a decreasing function, satiation and hunger are being modeled. When  $r$  is increasing, learning effects are being modeled. This new model will be referred to as the active response model.

The active response model is most easily analyzed when  $r$  takes the form

$$r(z) = \rho_0 z^v \quad \text{where } \rho_0 \text{ and } v \text{ are constants.}$$

This form does not allow saturation except when  $v = -1$  and so it is not realistic at high prey densities. However, for negative  $v$ , attack rates do decline as densities increase, mimicking the approach to saturation in more realistic models. Moreover at low densities, the form  $r(z) = \rho_0 z^v$  gives a total functional response that approximates the functional responses discussed by Real (1977) for one prey species.

### 3. BEHAVIOR OF THE AGGREGATE IN THE PRESENCE OF BETWEEN-INDIVIDUAL VARIATION

Phenotypic variation is a characteristic of biological populations and so it is likely that there will be variation from individual to individual in the

parameters of the functional response of a predator. For example, there is evidence that preference may vary considerably among the individuals in a predator population (Murdoch and Oaten, 1975). Such variation may be modeled by treating the parameters of the functional response as random variables. In a situation with  $n$  predator individuals, the mean rate of consumption of prey species  $i$  will be

$$nEf_i(H_1, H_2), \quad (6)$$

where  $E$  is the expected value taken with respect to the distribution of functional response parameters among individual predators. If  $n$  is large and the individuals are hunting independently, then (6) will be close to the actual number of prey species  $i$  consumed by the predator population in one unit of time. Indeed the law of large numbers says that the random deviation from (6) will be  $o(n)$  in probability, i.e., when this random deviation is divided by  $n$ , the result converges in probability to 0 as  $n \rightarrow \infty$ .

If  $n$  is not large the analysis given here still applies but with a different interpretation. For small  $n$  the symbol  $E$  must refer to the finite distribution of functional response parameters actually found in the small population. Then (6) is still close to the actual rate of consumption of species  $i$  provided the time interval involved is long enough for within-individual variability (P. L. Chesson, 1978) to be unimportant. This will be so when repeated observations on the same individual do not show much variation in consumption rates.

In either of the two situations discussed here, we are justified in regarding (6) as the functional response of the total predator population or the "population functional response." Below we shall also introduce the terms "population preference" and "population switching." By introducing these terms we simply wish to draw appropriate analogies between phenomena that occur at a population level, and phenomena that occur at an individual level. We do not wish to imply any thinking or decision making on the part of the population, just as preference and switching at the individual level do not imply thinking or decision making by individuals, even though individual decision making may be involved.

Except in the linear case the population functional response will generally be of a different form than the individual functional responses as a consequence of the well-known result that  $Ef(X)$  is generally different from  $f(EX)$  when  $f$  is nonlinear (e.g., P. L. Chesson, 1981). We shall see that this different functional form often gives population switching behavior. In the linear case, however, population switching behavior is not found because then  $Ef_i(H_1, H_2) = \rho(E\alpha_i) H_i$  so that the population functional response is also linear.

To investigate population switching behavior for the general case we consider the ratio of ratios

$$c^* = \frac{E f_1(H_1, H_2)}{E f_2(H_1, H_2)} \left/ \left( \frac{H_1}{H_2} \right) \right. \quad (7)$$

or equivalently  $\alpha_1^* = c^*/(1 + c^*)$ , which we shall call the population preference for species 1. Note that  $c^*$  and  $\alpha_1^*$  are defined in terms of the population functional response in just the same way that  $c$  and  $\alpha_1$  are defined in terms of individual functional responses. Population preference for species 2 is  $\alpha_2^* = 1/(1 + c^*)$ . Like individual preferences,  $\alpha_1^* + \alpha_2^* = 1$ . Using (2) we obtain

$$\alpha_1^* = \alpha_1^*(H_1, H_2) = \frac{E[f_T(H_1, H_2) \alpha_1 \{ \alpha_1 H_1 + \alpha_2 H_2 \}^{-1}]}{E[f_T(H_1, H_2) \{ \alpha_1 H_1 + \alpha_2 H_2 \}^{-1}]} \quad (8)$$

To convert (8) into a more workable expression define  $x = H_1/(H_1 + H_2)$  (relative density of species 1),  $y = H_1 + H_2$  (total absolute density), and

$$\Gamma(\alpha_1, x) = E\{f(x, y)/[\alpha_1 xy + \alpha_2(1-x)y] \mid \alpha_1\}. \quad (9)$$

Here  $f(x, y) = f_T(H_1, H_2)$  and  $y$  is suppressed in  $\Gamma(\alpha_1, x)$  for notational simplicity. We can now write (suppressing  $y$  again)

$$\alpha_1^*(x) = \frac{E \alpha_1 \Gamma(\alpha_1, x)}{E \Gamma(\alpha_1, x)}. \quad (10)$$

Expression (10) exhibits the population preference  $\alpha_1^*$  as a weighted average of the preferences of individuals. Moreover, except in the linear case, the weights are functions of relative density which immediately suggests that some kind of switching behavior ought to occur for the population. Indeed, intuition suggests the following sufficient, but not necessary, criteria: if  $\Gamma(a', x)/\Gamma(a, x)$  is an increasing function of  $x$  for  $a' > a$  then  $\alpha_1^*$  will be an increasing function of  $x$ , i.e., positive switching will occur. On the other hand, negative switching occurs if this ratio decreases with  $x$ . (If not obviously true, these statements follow from the general condition (12) below. See Appendix I for details.)

To determine when the above criteria will be satisfied, note that  $\Gamma(a', x)/\Gamma(a, x)$  increases or decreases with  $x$ , for  $a' > a$ , according to the sign of  $(\partial/\partial x)\{\log \Gamma(a', x) - \Gamma(a, x)\}/(a' - a)$ . Letting  $a' \rightarrow a$  we obtain

$$\frac{\partial^2}{\partial a \partial x} \log \Gamma(a, x). \quad (11)$$

Thus population switching behavior is given by the sign of (11), assuming that (11) has the same sign for all  $a$  and  $x$ . If the sign changes with  $x$ , but

not with  $a$ , then population preference will be increasing with  $x$ , for some values of  $x$ , and decreasing for others. Thus the graph of  $\alpha_1^*(x)$  need not be monotonic but can increase and decrease. In such cases switching behavior is defined locally, i.e., for a particular relative density  $x$ . On portions of the graph where  $\alpha_1^*(x)$  increases, we say positive switching occurs; where  $\alpha_1^*(x)$  decreases we say negative switching occurs. It is important to note that the switching behavior can also depend on  $y$ , the total absolute prey density. However, in spite of these various possibilities, in the model examples we give here, the same sort of switching behavior occurs at all relative and absolute densities, although the strength of the switching behavior can be very highly dependent on prey densities.

If it happens that the sign of (11) changes with  $a$ , then (11) does not determine population switching behavior and naturally the original criterion involving  $\Gamma(a', x)/\Gamma(a, x)$  fails also. However, a straightforward calculation shows that

$$\begin{aligned} \frac{\partial \alpha_1^*}{\partial x} &= \frac{E[\Gamma(\alpha_1, x) \alpha_1 (\partial/\partial x) \log \Gamma(\alpha_1, x)]}{E\Gamma(\alpha_1, x)} \\ &\quad - \frac{E[\Gamma(\alpha_1, x) \alpha_1] E[\Gamma(\alpha_1, x) (\partial/\partial x) \log \Gamma(\alpha_1, x)]}{(E\Gamma(\alpha_1, x))^2} \\ &= \mathcal{C}^\dagger \left( \alpha_1, \frac{\partial}{\partial x} \log \Gamma(\alpha_1, x) \right), \end{aligned} \quad (12)$$

where  $\mathcal{C}^\dagger$  stands for the weighted covariance with weights proportional to  $\Gamma(\alpha_1, x)$ . Thus to see if switching behavior is positive or negative, we ask whether on weighted-average  $(\partial/\partial x) \log \Gamma(\alpha_1, x)$  increases or decreases with  $\alpha_1$ . By way of comparison, when using criterion (11) we ask whether  $(\partial/\partial x) \log \Gamma(\alpha_1, x)$  is always increasing or always decreasing with  $\alpha_1$ , where "always" means "for all  $\alpha_1$  values." Thus criteria (11) and (12) are very closely related and will be difficult to distinguish in an experimental setting.

Our criteria for population switching behavior depend critically on the quantity  $\Gamma(\alpha_1, x)$ , which by definition is the conditional mean value, given  $\alpha_1$ , of

$$\frac{f(x, y)}{\alpha_1 x y + \alpha_2 (1-x) y}. \quad (13)$$

The numerator  $f(x, y)$  of (13) is the total functional response, while the denominator is proportional to the total functional response that occurs when the separate functional responses for the two prey species are linear. Changes in (13) as  $x$  and  $\alpha_1$  are varied result from nonlinearity of the actual functional responses. Expressions (11) and (12) can thus be regarded as



measures of nonlinearity of the functional responses. Since the linear response does not lead to population switching behavior it is not surprising that the criteria for population switching behavior involve such measures of nonlinearity.

Criteria (11) and (12) are applied to specific models in the next section. However, in some cases these criteria are too difficult to calculate and we must rely on a less informative analysis using the idea of *average* switching behavior. The quantity  $\partial\alpha_1^*/\partial x$  whose sign is indicated by (11) and (12), tells us the switching behavior for relative density changes in a small neighborhood of the given relative density  $x$ ; it gives the local switching behavior discussed above. On the other hand,

$$\int_0^1 \frac{\partial\alpha_1^*}{\partial x} dx = \alpha_1^*(1) - \alpha_1^*(0) \quad (14)$$

indicates the average switching behavior for all possible changes in relative density, at fixed total prey density. There are many different ways of taking an average. The particular method (14) gives the same weight to all relative densities.

To determine the sign of (14) we note from (10) that  $\alpha_1^*(x) > E\alpha_1$  or  $\alpha_1^*(x) < E\alpha_1$  depending on whether  $\alpha_1$  is positively or negatively correlated with  $\Gamma(\alpha_1, x)$ . If the sign of this correlation changes as  $x$  changes from 0 to 1, then the average switching behavior can be determined by this technique.

#### 4. SWITCHING BEHAVIOR WHEN PREFERENCE IS THE ONLY VARIABLE

To apply the criteria above to specific models we continue to assume that individuals have no switching behavior, but that different individuals have different preferences (between-individual variation in preference). When all between-individual variation in the functional responses comes from variation in preferences,  $\Gamma(\alpha_1, x)$  is equal to expression (13). Evaluating criterion (11) for the disk model we obtain

$$\frac{\partial^2}{\partial a \partial x} \log \Gamma(a, x) = - \frac{\rho y (\eta_1 + \eta_2) + (\rho y)^2 \eta_1 \eta_2}{\{1 + \rho y [a \eta_1 x + (1 - a) \eta_2 (1 - x)]\}^2}. \quad (15)$$

This quantity is always negative and so negative switching always occurs in the disk model. However, for small handling times ( $\eta_i$ ), small  $\rho$  (hunting rate during search time), or small  $y$  (total absolute density) the disk model is very close to the linear model and so in these cases the magnitude of the negative switching effect should be small and indeed this is reflected by a small absolute value for (15).

On the other hand, if handling times are large or  $\rho$  or  $y$  is large, the disk model is similar to the saturated disk model and expression (15) is close to the following value for the saturated disk model:

$$\frac{\partial^2}{\partial a \partial x} \log \Gamma(a, x) = - \frac{\eta_1 \eta_2}{\{a\eta_1 x + (1-a)\eta_2(1-x)\}^2}. \quad (16)$$

Clearly when both handling times are positive the saturated disk model also leads to negative switching at the population level.

To see if the negative switching effect is stronger at saturation, we note that when  $\eta_1 = \eta_2$ , (15) decreases to (16) as  $\rho$ ,  $y$ , or  $\eta_1$  and  $\eta_2$  increase. This suggests a stronger negative switching effect near saturation, but there is no direct correspondence between the magnitude of  $(\partial^2/\partial a \partial x) \log \Gamma(a, x)$  and the magnitude of the negative switching effect. Furthermore when  $\eta_1 \neq \eta_2$  the behavior of (15) is dependent on the relative density and preference values involved. More reliable information comes from  $\alpha_1^*(1) - \alpha_1^*(0)$  which gives the average switching behavior. In Appendix II it is shown that the magnitude of the average negative switching behavior is always greatest near saturation.

Although average switching behavior appears to give a clear conclusion, some caution is necessary. For example, when one of the handling times is zero, the value of  $\alpha_1^*(1) - \alpha_1^*(0)$  in the saturated disk model is different from the limiting value given by the disk model as saturation is approached. Indeed the saturated disk model shows no switching behavior at saturation, when one handling time is 0, while the disk model continues to show the maximum average negative switching effect on the approach to saturation. This discontinuity is explained by the behavior of (15) as saturation is approached. If  $\eta_1 = 0$ , then (15) converges to 0 for all  $x < 1$ , indicating that  $\partial \alpha_1^*/\partial x$  converges to 0 for relative densities less than 100%. However, for  $x = 1$ , expression (15) converges to  $-\infty$  reflecting the fact that  $\partial \alpha_1^*/\partial x$  converges to  $-\infty$  for  $x = 1$  (Appendix II). Thus near saturation the negative switching effect is confined to a small interval of relative density near 100% of species 1. However, the magnitude of the effect in this interval is very large so that  $\alpha_1^*(1) - \alpha_1^*(0)$  actually increases as saturation is approached. Since it is very difficult to measure preference when one species is present almost exclusively, this extreme negative switching near  $x = 1$  is likely to be undetectable experimentally and the total absence of negative switching in the saturated disk model gives a good indication of what is likely to be seen in the real world.

The conclusions above with one handling time 0 generally indicate the situation that applies when both handling times are positive but markedly different from one another (Appendix II). When handling times are very different, most of the negative switching effect found near saturation occurs over a very small range of relative densities. For relative densities outside

this range it seems likely that the negative switching effect will actually decline as saturation is approached even though there must be an increase for the average of all relative density changes.

For the active response model the criterion (11) is difficult to use without specification of  $r$ . Because of this problem we first apply (11) to a special form of  $r$  and use a more limited analysis for the general case. Assuming that  $r(z) = z^\nu \rho_0$  for constants  $\nu$  and  $\rho_0$  we obtain

$$\frac{\partial^2}{\partial a \partial x} \log \Gamma(a, x) = \frac{\nu v_1 v_2}{[a v_1 x + (1 - a) v_2 (1 - x)]^2}, \quad (17)$$

and so population switching behavior is negative or positive depending on the sign of  $\nu$ . Negative  $\nu$ , giving negative switching, is the model of satiation effects, while positive  $\nu$ , with positive switching, is our model of learning effects and gives a type III functional response. It should be kept in mind that regardless of the particular function  $r$ , no individual switching occurs—all of the switching behavior seen here is at the population level.

For general  $r$  we have  $\Gamma(\alpha_1, x) = r(\alpha_1 v_1 x y + \alpha_2 v_2 (1 - x) y)$ . If  $r$  is a decreasing function and we define  $x^* = v_2 / (v_1 + v_2)$ , then  $\Gamma(\alpha_1, x)$  is an increasing function of  $\alpha_1$  for  $x < x^*$  and a decreasing function for  $x > x^*$ . From the discussion in Section 3 this means that

$$\alpha_1^*(x^* + \varepsilon_1) < E\alpha_1 < \alpha_1^*(x^* - \varepsilon_2)$$

for positive  $\varepsilon_i$ . In particular  $\alpha_1^*(1) < \alpha_1^*(0)$  so that negative switching occurs here in the general model of satiation. Conversely if  $r$  is an increasing function, learning effects are being modeled and positive switching occurs.

Situations in which learning is important at low absolute densities and satiation at high absolute densities are likely in the real world. These will mean that positive switching will occur for small  $y$  while negative switching will occur for large  $y$ , all of these effects being at the population level.

### 5. EXPLANATION OF POPULATION SWITCHING BEHAVIOR IN TERMS OF WEIGHTED AVERAGES

In the examples above, negative switching occurs where the total functional response  $f(x, y)$  varies less with prey relative density and prey preference than the total linear response. The latter is proportional to  $\alpha_1 x + \alpha_2 (1 - x)$ . To see what is happening here, it is instructive to examine in detail the case where  $f(x, y)$  is independent of the relative density. This is not realistic for small  $y$  but provides a simple illustration to explain the effects we see. Examples where  $f(x, y)$  is independent of  $x$  are the saturated

disk model with  $\eta_1 = \eta_2$  and the active response model with  $\nu = -1$  and  $v_1 = v_2$ . The population preference is given by

$$\alpha_1^* = \frac{E\alpha_1[\alpha_1 x + \alpha_2(1-x)]^{-1}}{E[\alpha_1 x + \alpha_2(1-x)]^{-1}}. \quad (18)$$

Consider two individuals,  $A$  with a high  $\alpha_1$  and  $B$  with a low  $\alpha_1$ . In expression (18),  $A$  gets more weight than  $B$  at low  $x$  values. The reason is that the linear response predicts  $A$  will not consume many prey at low  $x$  values, but with constant  $f$ ,  $A$  has the same total prey consumption at all  $x$  values. It follows that  $A$  with constant  $f$  appears like several  $A$ 's with linear  $f$ . Conversely  $B$  with constant  $f$  appears like less than one  $B$  with linear  $f$ . Thus at low  $x$  the population preference will be more than the average preference  $E\alpha_1$ , which is the population preference for the linear response. Conversely at high  $x$  the population preference is greater than the average preference. Thus negative switching must occur.

The above explanation of population negative switching applies generally in the situation where  $f$  tends to vary less with relative density and preference than the linear response predicts. On the other hand, in the case where  $f$  tends to vary more with relative density and preference than predicted by the linear response, population positive switching occurs. Indeed criteria (11) and (12) are the precise mathematical statements of these qualitative remarks.

## 6. SWITCHING BEHAVIOR WHEN PREFERENCE IS NOT THE ONLY VARIABLE

Section 4 considered switching behavior for the case where individuals differ only in their preferences. It is clear from (10) that between-individual variation of preference is essential to population switching behavior, but does variation in other parameters of the functional response significantly alter the results obtained above? This is important because other parameters of the functional response may well vary just as much or more than preference and these parameters may be correlated with preference in various ways.

Data on the backswimmer *Notonecta hoffmani* preying on mosquito larvae and *Daphnia* (J. Chesson, pers. comm.) show wide variation in both preference and handling times of mosquitoes among the 19 predator individuals but there is no significant correlation between preference and handling time ( $p > 0.25$ ). I know of no other data on covariation of preference with handling time and the causes and natures of such covariation are likely to be varied and difficult to determine. Thus in the analysis below we recognize that there may be relationships among the different parameters without attempting to justify any particular relationships.

Consider just the disk model. To model variation in the parameters let  $\rho = \phi_0(\alpha_1) \gamma_0$ ,  $\alpha_i \eta_i = \phi_i(\alpha_1) \gamma_i$ ,  $i = 1, 2$ . Here  $\phi_0$ ,  $\phi_1$ , and  $\phi_2$  are fixed functions;  $\gamma_0$ ,  $\gamma_1$ ,  $\gamma_2$  are random variables independent of the  $\alpha_i$ , and they are assumed to have mean 1. This model permits the conditional means of  $\rho$  and  $\eta_i$  to depend in a completely general way on  $\alpha_i$  but imposes a multiplicative model for variation about the conditional mean.

To determine average switching behaviour note that

$$\Gamma(\alpha_1, x) = E[\rho / \{1 + \rho y[\alpha_1 \eta_2 x + \alpha_2 \eta_2(1 - x)]\} | \alpha_1]. \quad (19)$$

Substituting for  $\rho$  and  $\eta_i$ , keeping  $\alpha_1$  fixed at  $a$  and defining  $\Delta_1 = 1$ ,  $\Delta_2 = 0$ , we get

$$\Gamma(a, \Delta_i) = E\phi_0(a) \gamma_0 / \{1 + y\phi_0(a) \phi_i(a) \gamma_0 \gamma_i\}. \quad (20)$$

To see how this varies with preference,  $a$ , we calculate

$$\frac{\partial}{\partial a} \Gamma(a, \Delta_i) = E \frac{\phi_0'(a) \gamma_0 - y\phi_0^2(a) \phi_i'(a) \gamma_i \gamma_0^2}{[1 + y\phi_0(a) \phi_i(a) \gamma_0 \gamma_i]^2}. \quad (21)$$

For large  $y\phi_0(a) \phi_i(a)$ , or small  $(\log \phi_0(a))' / (\log \phi_i(a))'$ , the second part of the numerator is dominant and we have

$$\frac{\partial}{\partial a} \Gamma(a, \Delta_i) \simeq -E \frac{y\phi_0^2(a) \phi_i'(a) \gamma_i \gamma_0^2}{[1 + y\phi_0(a) \phi_i(a) \gamma_0 \gamma_i]^2}. \quad (22)$$

Our discussion is based on this approximation, which is applicable near saturation of the function responses, or in situations where  $\rho$  is much less dependent on preference than are the products of preference and handling time.

Now  $\alpha_1^*(\Delta_i) - E\alpha_1$  has the same sign as the correlation between  $\Gamma(\alpha_1, \Delta_i)$  and  $\alpha_1$ , which, from (22), has the same sign as  $-\phi_i'(\alpha_1)$ . This means that  $\alpha_1^*(0) > \alpha_1^*(1)$  (i.e., negative switching occurs) whenever  $E[\alpha_i \eta_i | \alpha_i]$  is an increasing function of  $\alpha_i$ ,  $i = 1, 2$ . Positive switching occurs when  $E[\alpha_i \eta_i | \alpha_i]$  is a decreasing function of  $\alpha_i$ ,  $i = 1, 2$ . Thus in contrast to the situation where only the preferences vary among individuals, here it is possible to get positive switching. However, positive switching does not seem a very likely possibility for it requires handling time to decrease very rapidly with increasing preference. Negative switching is the most likely possibility in this model for it occurs when handling time is independent of preference, increases with preference, or when the conditional mean handling time declines with increasing preference at a slower rate than  $1/\alpha_i$ .

The effect of variability in the hunting rate parameter  $\rho$  is difficult to assess when  $y$  is not large and  $\rho$  is strongly dependent on preference. The analysis above shows that variation in  $\rho$  independent of  $\alpha_1$  does not affect

our previous conclusions in any way. Moreover if  $\rho$  does not depend strongly on preference, any effect it might have is not important for large absolute densities, i.e., near saturation, where the strongest negative switching effects are often found.

In summary, although variation in handling time and hunting rate produces some modification of our previous results, no striking differences are apparent.

## 7. THE MAGNITUDE OF POPULATION SWITCHING BEHAVIOR

A theoretical analysis that demonstrates the existence of some tendency in a system is not complete until the strength of that tendency has been evaluated. Thus we must explore the strength of the population switching behavior demonstrated above and to do this we must evaluate  $\alpha_1^*$  as a function of  $x$ .

In general,  $\alpha_1^*$  cannot be evaluated analytically and numerical methods are necessary. Numerical methods require an explicit model for variation in  $\alpha_1$ . The beta distributions (Johnson and Kotz, 1970) provide a suitable model because by varying the parameters they can be made to take on a variety of plausible forms. The beta density is

$$f(\alpha) = \alpha^{\beta_1-1}(1-\alpha)^{\beta_2-1}/B(\beta_1, \beta_2), \quad (23)$$

$\alpha \in (0, 1)$ .  $B(\beta_1, \beta_2)$  is the beta function and  $\beta_1$  and  $\beta_2$  are positive parameters. By varying these parameters we can obtain distributions with a single mode in  $(0, 1)$ , U-shaped distributions and J-shaped distributions.

The figures give  $\alpha_1^*$  as a function of relative density ( $x$ ). Figures 1 and 2 are for the saturated disk model with equal handling times ( $\eta_1 = \eta_2$ ). In Fig. 1,  $\beta_1 = \beta_2$  and the distribution of  $\alpha_1$  is symmetrical about  $\frac{1}{2}$ . Figure 2 is for asymmetrical distributions of preference.

In Fig. 1, curves a-e show how the negative switching effect increases with the variance of  $\alpha_1$ . Curve a is for a distribution with a mode at  $\frac{1}{2}$  while curves b-e are for progressively more extreme U-shaped distributions. Distribution e is the limiting case where preference can only be 0 or 1. The figure shows that the negative switching effect is only significant when  $\alpha_1$  has a high variance.

Figures 3 and 4 for disk model. Both are for U-shaped distributions of preference where the switching behavior is most significant. However, in Fig. 4 the variance of preference is higher and the switching effects are more pronounced. Curves a-c were calculated assuming that handling times are equal and nonrandom so that

$$\alpha_1^* = \frac{E\alpha_1\{1 + \rho y \eta[\alpha_1 x + \alpha_2(1-x)]\}^{-1}}{E\{1 + \rho y \eta[\alpha_1 x + \alpha_2(1-x)]\}^{-1}}. \quad (24)$$

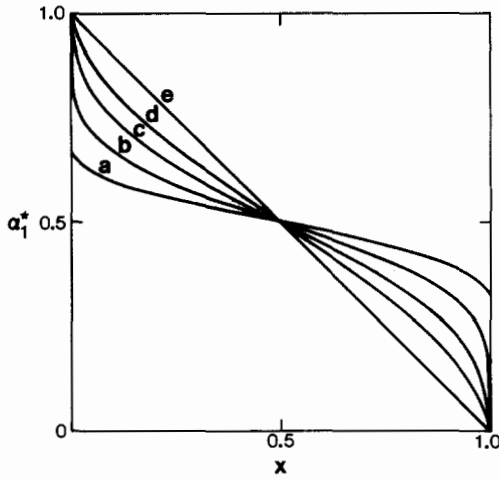


FIG. 1. Population switching behavior in the saturated disk model. (a)  $\beta_1 = \beta_2 = 2$ , (b)  $\beta_1 = \beta_2 = 1$ , (c)  $\beta_1 = \beta_2 = 0.5$ , (d)  $\beta_1 = \beta_2 = 0.25$ , (e)  $\beta_1 = \beta_2 = 0$ .

In this formula  $\rho y \eta$  can be treated as a single parameter determining the degree of saturation of the functional response. Comparisons a–c show the change with increasing saturation. Curve d differs from the others by having handling time a function of preference. The model here is  $\eta_i = k\alpha_i^{-2}$ , where  $k$  is a constant, and shows the theoretically predicted positive switching effect when handling time decreases rapidly with increasing preference.

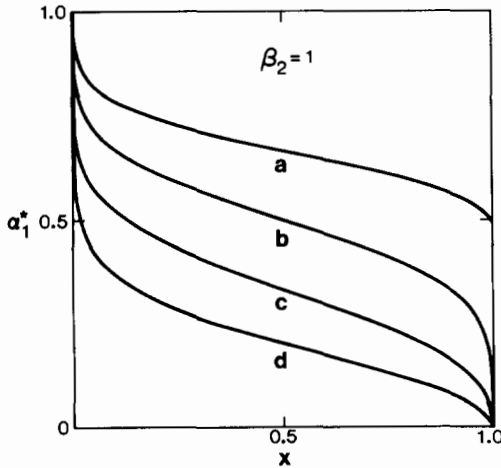


FIG. 2. Population switching behavior in the saturated disk model with asymmetrical distributions of preference. For all curves  $\beta_2 = 1$ . (a)  $\beta_1 = 2$ , (b)  $\beta_1 = 1$ , (c)  $\beta_1 = 0.5$ , (d)  $\beta_1 = 0.25$ . As  $\beta_1$  is decreased the distributions become more J-shaped.

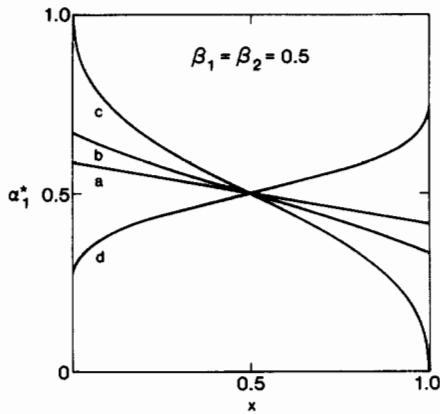


FIG. 3. Population switching behavior in the disk model. (a)  $\rho\gamma\eta = 1$ , (b)  $\rho\gamma\eta = 3$ , (c)  $\rho\gamma\eta = \infty$ , (d)  $\eta_i = k\alpha_i^{-2}$ ,  $\rho\gamma k = 3$ .

Taken together the curves show that in the disk model the biologically significant switching behavior is to be found near saturation. The curves are for highly variable preferences because only then do the numerical calculations show significant effects. If preferences are only moderately variable the switching behavior will be minor. However, our study is justified by the highly variable distributions of preference found in nature (Murdoch and Oaten, 1975), and the presence of population negative switching in some data from Murdoch (1969) which we now discuss.

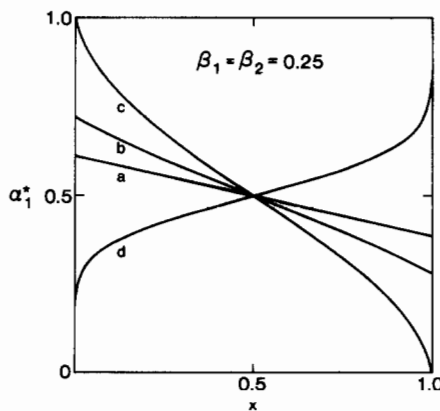


FIG. 4. Population switching behavior in the disk model. (a)  $\rho\gamma\eta = 1$ , (b)  $\rho\gamma\eta = 3$ , (c)  $\rho\gamma\eta = \infty$ , (d)  $\eta_i = k\alpha_i^{-2}$ ,  $\rho\gamma k = 3$ .



### 8. EXPERIMENTAL EVIDENCE FOR POPULATION NEGATIVE SWITCHING

The first investigation of predator switching, viz., Murdoch (1969), contains evidence of population negative switching. Murdoch set out to test the idea that high variability in preference is indicative of lability of preference, and that this lability should lead to positive individual switching as prey densities are varied. Using the whelk *Acanthina* preying on barnacles and mussels, Murdoch found high variability in preference but only under special circumstances did he observe positive switching. These special circumstances involved training the predators on a pure diet of the more abundant prey species before exposing them to a mixture of the two prey species to assess their preferences. However, a reanalysis of the data for untrained predators reveals population negative switching (Fig. 5).

Each point in Fig. 5 is an estimated  $\alpha_1^*$  value, denoted by  $\hat{\alpha}_1^*$  and calculated according to the formula

$$\hat{\alpha}_1^* = \frac{X_1(1-x)}{X_1(1-x) + X_2x}, \quad (25)$$

where  $X_i$  is the total consumption of prey species  $i$  by the 10 individuals exposed to relative density  $x$  of species 1 (barnacles). The fit to a linear

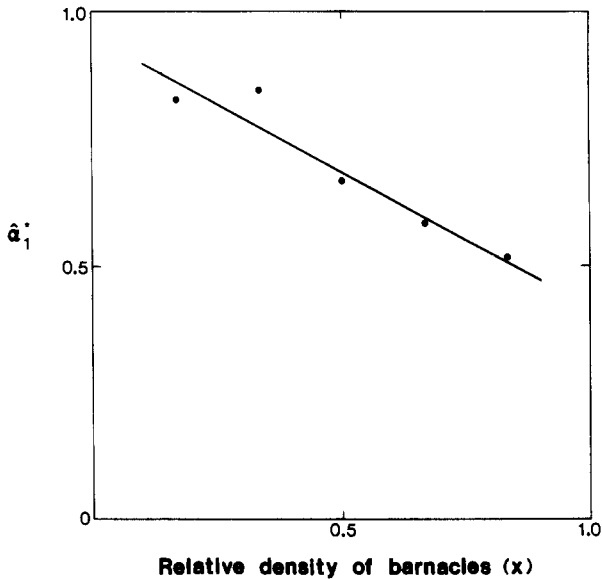


FIG. 5. Population negative switching for *Acanthina* preying on barnacles and mussels. See text for explanation.

regression is good ( $r^2 = 0.92$ ,  $p < 0.01$ ) and this is in accordance with the theoretical curves (Figs. 1–4) which are approximately linear except at high and low relative densities.

In order to confirm that the negative switching shown in Fig. 5 is not a consequence of individual negative switching we need to examine the behavior of individuals. This cannot be done directly with Murdoch's data because his experiments involved pairs of individuals and so the best we can do is examine the preferences of groups of two individuals. However, from this we can extrapolate to the individual level.

Figure 6 plots the  $\hat{\alpha}_i^*$  values calculated for each pair of individuals. The regression of  $\hat{\alpha}_i^*$  against relative density has a slope of  $-0.270$  which is about one-half of the slope  $-0.536$  found for groups of 10 individuals; however, the slope in Fig. 6 is not statistically significantly different from 0 ( $p > 0.25$ ).

Note that in Murdoch's experiments a different group of predator individuals was used for each relative density. Thus to interpret Fig. 6 we need to develop some theory applicable to small groups of predators where observation is made on a different small group at each prey relative density.

To develop the required theory let  $X_{in}$  be the consumption of prey species  $i$  by a group of  $n$  predator individuals. As a simple consequence of Eqs. (2) and (8) we see that

$$EX_{in} = nEf_i(H_1, H_2) = nK(x, y) \alpha_i^*(x, y) H_i, \quad (26)$$

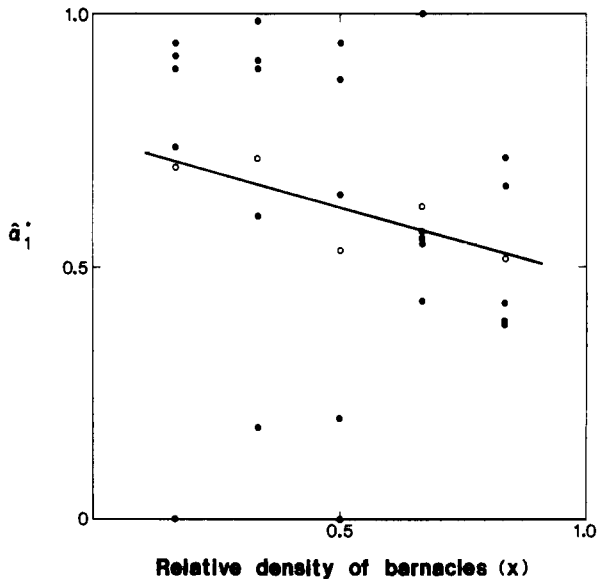


FIG. 6. Group preferences calculated for pairs of *Acanthina* preying on barnacles and mussels (●), ○, the means.

where  $\alpha_i^*(x, y)$  is the population preference for the effectively infinite population from which the group of  $n$  individuals is drawn and  $K(x, y)$  is some function of  $x$  and  $y$  that does not depend on the prey species  $i$ . For large  $n$  the moment estimator

$$\hat{\alpha}_{1n}^* = \frac{X_{1n}(1-x)}{X_{1n}(1-x) + X_{2n}x} \quad (27)$$

will be close to  $\hat{\alpha}_1^*$  by the law of large numbers, but  $\hat{\alpha}_{1n}^*$  will rarely be an unbiased estimator of  $\alpha_1^*$ , i.e.,  $E\hat{\alpha}_{1n}^* \neq \alpha_1^*$ .

For small  $n$  this bias may be appreciable and in particular for  $n = 1$ , (27) is the standard estimate of preference of an individual (J. Chesson, 1978). Thus for  $n = 1$ , (27) is estimating individual preference rather than population preference. With sufficient observations on an individual, as discussed below,  $E\hat{\alpha}_{1,1}^*$  will be close to  $E\alpha_1$ , the unweighted average of individual preferences for the entire population. Individual switching behavior will thus be determined by the regression of  $\hat{\alpha}_{1,1}^*$  on relative density, provided of course that all individuals show the same kind of behavioral response to relative density changes.

To estimate the regression of  $\hat{\alpha}_{1,1}^*$  on relative density we note that, to a rough approximation, the bias in (27) is of the form  $A/n$  (Cox and Hinkley, 1974), with  $A$  a function of  $x$  and  $y$ . It follows that the bias in the slope of the regression of  $\hat{\alpha}_{1n}^*$  on  $x$  is approximately of the form  $a/n$  and so the difference in expected slopes for the regression of  $\hat{\alpha}_{1,10}^*$  and  $\hat{\alpha}_{1,2}^*$  is  $0.4a$ . Thus from Figs. 5 and 6 we get 0.665 as an estimate of  $a$ . Using this estimate of  $a$  and the slope  $-0.536$  for the regression of  $\hat{\alpha}_{1,10}^*$  we obtain 0.063, as an estimate of the slope of the regression of  $\hat{\alpha}_{1,1}^*$ . This estimated slope is near enough to 0. Thus the data provide no evidence of individual switching behavior, which suggests that the negative switching seen for groups of size 10 is mostly due to variation between individuals. The data are not sufficient to rule out individual switching behavior, but the figures show that variability is quite high, and since Figs. 5 and 6 were calculated from the same data, this variability is the only explanation for the observed difference between the regressions. Thus we can be confident that the phenomena discussed in this paper are operating.

## 9. IMPLICATIONS FOR METHODOLOGY AND DATA ANALYSIS

Ecological investigations are mainly concerned with outcomes at the population level. Studies of the behavior of individuals are often used to infer such outcomes. However, when individuals vary in quantitative aspects of individual behavior, we have seen that the qualitative outcome at the

population level may be quite different from that suggested by the qualitative aspects of individual behavior. In this study the population shows switching behavior because at different prey relative densities, different individuals with different preferences become prominent in determining the population preference. Thus changes at the population level may reflect changes in the relative importance of different individuals to the population outcome rather than any changes at the individual level. Thus when trying to infer population behavior from individual behavior it is important to take into account the effects of variation between individuals. Conversely when trying to explain population behavior in terms of individual behavior the possible effects of variation between individuals must be considered.

To determine population behavior the most reliable method is to study a group of individuals and the group should be large enough that the biases discussed in the previous section are not important. The approximation  $A/n$  for the bias for a group of size  $n$  suggests that a  $(100A/n)\%$  bias will be found for the deviation between population and individual behavior and this will be unimportant for moderately large  $n$ .

If the group is studied for fixed periods of time, with negligible prey depletion, then formula (27) can be used to estimate the population preference. To explain the outcome it is necessary to record the meals of individuals and to calculate individual preferences. In this way the effect of individual behavior can be distinguished from the effect of between-individual variation.

To study individual switching behavior, it would be best to study each individual at a range of prey relative densities. Switching behavior can then be determined for each individual using the methods reviewed by J. Chesson (1983). Some difficulties with studying individuals in this way may arise because individuals are sensitive to previous history so that the order in which the experiments are done, and the times between them, may affect the outcome. Moreover it may not be possible to collect sufficient information on an individual to get a good estimate of its preference at each prey relative density.

When each individual is observed at only one prey relative density, it is only possible to infer individual switching behavior if most individuals have the same qualitative behavior, i.e., most switch positively, most switch negatively, or most have no switching behavior. Then  $E\alpha_1$  will reflect individual switching behavior; and this quantity can be estimated by the simple arithmetic mean  $\bar{\alpha}_1$  of each individual's estimated preference at given prey densities.

It is important to note that other methods of arriving at an average preference value for the individuals in the population may actually estimate some quantity that is neither population preference nor the mean individual preference. For example, data for individuals are often converted to

percentages that a prey makes up of the diet. If least-squares regression techniques are used to analyze these percentages or the percentages are averaged to calculate an overall preference value, then a bias in the direction of negative switching is likely to be introduced regardless of whether negative switching occurs at the population level. This occurs because a preference value calculated from the average of the percentages behaves like a population preference for a population in which the individuals have saturated functional responses and equal handling times. Thus our work above suggests that a component of negative switching will be added to preferences calculated in this way. The same phenomenon can occur, and for the same reasons, if observation on each individual involves a fixed total number of prey captures and the absolute number of captures for each individual are summed for each prey species, and these totals are then used in a least squares regression or are converted to preference values. A possible result in both of these cases is that positive individual switching will be masked by the bias in the direction of negative switching introduced in the analysis.

Other biases can be introduced if there is very little data on each individual for then  $\bar{\alpha}_1$  may be a biased estimate of  $E\alpha_1$ . Manly (1974) gives approximate bias formulas for two different experimental situations. To see how such biases can give the appearance of switching behavior, consider the situation where preferences are measured at constant prey densities and there is no individual switching behavior. Then simple arguments (J. Chesson, 1978) lead to a binomial distribution for the number of species 1 consumed, given the total consumption. It follows that the mean proportion of the diet coming from species 1 is

$$EP_1 = \frac{\alpha_1 x}{\alpha_1 x + \alpha_2(1-x)}, \tag{28}$$

and the maximum likelihood estimate of  $\alpha_1$  is

$$\hat{\alpha}_1 = \phi_x(P_1) = \frac{P_1(1-x)}{P_1(1-x) + (1-P_1)x}. \tag{29}$$

Now  $\phi_x(EP_1) = \alpha_1$  and  $\phi_x$  is convex for  $x > \frac{1}{2}$ , and concave for  $x < \frac{1}{2}$ . Jensen's inequality implies that  $E\hat{\alpha}_1 > \alpha_1$  for  $x > \frac{1}{2}$  and  $E\hat{\alpha}_1 < \alpha_1$  for  $x < \frac{1}{2}$ . Thus  $\hat{\alpha}_1$  is biased in such a way that the data may appear to show positive switching. The precise formula for the bias is very complicated but it is shown in Appendix III that

$$\frac{d}{dx} E\hat{\alpha}_1 |_{x=0.5} = \frac{4\alpha_1\alpha_2}{m}, \tag{30}$$

where  $m$  is the total number of prey consumed of both species. Expression (30) gives the expected slope at  $x = \frac{1}{2}$  for the regression of  $\hat{a}_1$  on  $x$ . Thus for prey relative densities near 50%, expression (30) measures the magnitude of the apparent switching effect introduced by bias in the estimator.

Note that (30) has a maximum value of  $1/m$  for  $\alpha_1 = \alpha_2 = \frac{1}{2}$  and so with a moderate number of observations on an individual the bias will be quite small. However, if very few observations are made on each individual and this lack of data on individuals is compensated for by observing many individuals, then positive switching may appear to be occurring when in fact there is none either at the individual or population levels.

The data from Murdoch (1969), reanalyzed above, involved 10–38 observations per pair of individuals, with a mean of 22. While the binomial model above is not directly applicable it still suggests that bias due to a small number of observations per individual is not likely to be a significant problem with Murdoch's data.

## 10. IMPLICATION FOR POPULATION DYNAMICS

Positive switching is thought to be a factor involved in stabilizing prey populations because it may act to increase per capita mortality due to predation as prey density increases (Murdoch, 1969; Murdoch and Oaten, 1975; Oaten and Murdoch, 1975; Murdoch, 1977; Tansky, 1978). Negative switching may act in the opposite manner by increasing the per capita predation rate as prey density decreases. Thus it is likely to destabilize prey populations: essentially it will tend to reinforce fluctuations in the density of one prey relative to the other and increase the chance of local extinction of one prey species. Since negative switching acts to the detriment of the rarer species, whichever that may be, it is likely to reinforce tendencies toward random exclusion of one of the two prey species as occurs in cases of Lotka–Volterra competition and in cases of the lottery model of Chesson and Warner (1981).

Although individual negative switching may occur (e.g., Reed, 1971) the results in this paper give a simple mechanism for population negative switching. Moreover population negative switching may commonly occur when preference is highly variable, food is sufficiently abundant that functional responses are near saturation, and individuals have no switching behavior. These last two conditions may well tend to occur together in nature. For example, in the linear model or the disk model, individual switching often has the effect of reducing the decline in food consumption as a preferred prey becomes relatively less abundant. However, this effect is much less near saturation and may even be reversed. Thus the benefit that an individual derives from switching may be reduced at high absolute densities

of prey. In addition, mechanisms for individual positive switching that involve spending little time in patches with low absolute prey densities (Murdoch *et al.*, 1975; Murdoch, 1977) may not operate when absolute densities are always high. If different individuals also tend to forage in different patch types or different subhabitat types with distinct prey, then the requirement of high variation in preference will be found. The experiments of Murdoch *et al.* (1975) appear to have all of these ingredients. Positive individual switching was found at very low absolute densities of prey, but the crucial experiments for our thesis, at high absolute density, were not done.

We have been concerned mostly with outcomes at the population level. Thus we are dealing with the level relevant to population dynamics. Individual switching behavior is only important to population dynamics to the extent to which it contributes to switching behavior at the population level. Although we have been mostly concerned with the case where individuals have no switching behavior it is clear that the effects discussed here overlay individual switching behavior and modify its outcome at the population level.

### APPENDIX I

Let  $\alpha_1$  have positive variance. We wish to prove that the weighted covariance (12) is positive if  $\Gamma(a', x)/\Gamma(a, x)$  is increasing in  $x$  for  $a' > a$ . Assuming differentiability,  $\Gamma(a', x)/\Gamma(a, x)$  is increasing in  $x$ , for  $a' > a$ , if and only if

$$\frac{\partial}{\partial x} \log \Gamma(a', x) - \frac{\partial}{\partial x} \log \Gamma(a, x) > 0 \tag{A1}$$

for  $a' > a$ . This implies that

$$\left[ \frac{\partial}{\partial x} \log \Gamma(\alpha_1, x) - \frac{\partial}{\partial x} \log \Gamma(E^\dagger \alpha_1, x) \right] [\alpha_1 - E^\dagger \alpha_1] \tag{A2}$$

is nonnegative, and is positive whenever  $\alpha_1 \neq E^\dagger \alpha_1$ . ( $E^\dagger Y = \text{def } EY\Gamma(\alpha_1, x)/E\Gamma(\alpha_1, x)$ , the weighted expected value of  $Y$ .) The weighted expected value of (A2) is the weighted covariance (12). Thus this weighted covariance is positive if  $\Gamma(a', x)/\Gamma(a, x)$  increases in  $x$ , for  $a' > a$ . Similarly if  $\Gamma(a', x)/\Gamma(a, x)$  decreases in  $x$ , for  $a' > a$ , then (12) is negative.

### APPENDIX II

To distinguish the disk model and the saturated disk models we shall add the subscripts d and s, respectively.

For the disk model we have

$$y\Gamma_d(\alpha_1, x) = \frac{\rho y}{1 + \rho y \{\alpha_1 \eta_1 x + \alpha_2 \eta_2 (1 - x)\}}. \quad (\text{A3})$$

Since this is a bounded continuous function of  $x$  and  $\alpha_1$  for fixed  $y$ , it follows that  $\alpha_{1d}^*(x)$  is continuous on  $[0, 1]$ . The derivative  $(\partial/\partial x)y\Gamma_d(\alpha_1, x)$  is also a bounded continuous function and so  $\alpha_{1d}^*(x)$  is differentiable, its derivative is given by (12), and (14) is satisfied. These properties of  $\alpha_{1d}^*(x)$  are important to ensure that analyses involving average switching behavior make sense.

If  $\eta_1$  and  $\eta_2$  are both positive,  $y\Gamma_d$  converges to  $y\Gamma_s$  as  $y \rightarrow \infty$ . Note that

$$y\Gamma_s(\alpha_1, x) = \{\alpha_1 \eta_1 x + \alpha_2 \eta_2 (1 - x)\}^{-1}. \quad (\text{A4})$$

Applying the monotone convergence theorem we see that  $\alpha_d^* \rightarrow \alpha_s^*$ . Thus for positive handling times, the limiting behavior of the disk model is given by the saturated disk model.

To see that the average switching effect is stronger near saturation we note that

$$\alpha_{1d}^*(1) = \frac{E\rho y \alpha_1 \{1 + \rho y \eta_1 \alpha_1\}^{-1}}{E\rho y \{1 + \rho y \eta_1 \alpha_1\}^{-1}} \quad (\text{A5})$$

and that

$$\lim_{y \rightarrow \infty} \alpha_{1d}^*(1) = \alpha_{1s}^*(1) = (E\alpha_1^{-1})^{-1} \quad (\text{A6})$$

which is the harmonic mean of  $\alpha_1$ . To see that (A6) is less than (A5) we note that  $\alpha_1 \{1 + \rho y \eta_1 \alpha_1\}^{-1}$  is a strictly increasing function of  $\alpha_1$  and therefore has a negative correlation with  $\alpha_1^{-1}$ . It follows that

$$E\{1 + \rho y \eta_1 \alpha_1\}^{-1} < E\alpha_1^{-1} E\alpha_1 \{1 + \rho y \eta_1 \alpha_1\}^{-1},$$

assuming of course that  $\alpha_1$  is nondegenerate. A simple rearrangement shows that (A6) is less than (A5). By symmetry it follows that  $\lim_{y \rightarrow \infty} \alpha_{2d}^*(0) > \alpha_{2d}^*(0)$  and so we have

$$\alpha_{1d}^*(1) - \alpha_{1d}^*(0) > \lim_{y \rightarrow \infty} \alpha_{1d}^*(1) - \alpha_{1d}^*(0). \quad (\text{A7})$$

Thus the negative switching effect is greatest near saturation.

When  $\eta_1 = 0$  the above analysis does not apply, for then  $\alpha_{1d}(1) = E\alpha_1$  for all  $y$ . However, if  $\eta_2 \neq 0$  it is still true that  $\lim_{y \rightarrow \infty} \alpha_{2d}^*(0) > \alpha_{2d}^*(0)$  and we see that (A7) still applies. However, average switching behavior is to some extent misleading here. To see this note when  $\eta_1 = 0$  we have

$$\alpha_{1s}^*(x) = \frac{E\alpha_1 \alpha_2^{-1}}{E\alpha_2^{-1}} = 1 - (E\alpha_2^{-1})^{-1}$$



and  $\alpha_{1d}^*(x) \rightarrow \alpha_{1s}^*(x)$  for  $x < 1$ . Moreover it can be shown that  $\partial\alpha_{1d}^*/\partial x \rightarrow 0$  as  $y \rightarrow \infty$  for  $x < 1$ . However, direct calculation shows that

$$\left. \frac{\partial\alpha_{1d}^*}{\partial x} \right|_{x=1} = \rho y \eta_2 (E\alpha_1 \alpha_2 - E\alpha_1 E\alpha_2) = -\rho y \eta_2 \mathcal{V} \alpha_1 \quad (\text{A8})$$

where  $\mathcal{V}$  means variance. Thus  $(\partial\alpha_{1d}^*/\partial x)|_{x=1} \rightarrow -\infty$  as  $y \rightarrow \infty$ . In summary, for the disk model with one zero handling time, the negative switching effect disappears as saturation is approached except when the prey species with 0 handling time is much more abundant than the other species. In these latter circumstances a strong negative switching effect will be seen and this effect is so great that the average switching behavior in  $(0, 1)$  is still found to be greatest near saturation.

The behavior of the disk model when one handling time is zero indicates the sort of behavior to be expected when both handling times are positive but markedly different. To see this we can use the convergence of the disk model to the saturated disk model. If  $\eta_1$  is relatively very small then inspection of the expression for  $\alpha_{1s}^*(x)$  shows that it will vary very little with  $x$  provided  $x$  is not near 1, but as  $x$  approaches 1 the dependence of  $\alpha_{1s}^*$  on  $x$  becomes quite pronounced. Near saturation  $\alpha_{1d}^*$  will behave similarly and so we see that the negative switching effect will be mostly confined to values of  $x$  near 1.

### APPENDIX III:

#### THE BIAS IN ESTIMATES OF INDIVIDUAL SWITCHING

The random variable  $mP_1$  is binomial with

$$P(mP_1 = j) = p(j, x) = \binom{m}{j} p^j(x)(1 - p(x))^{m-j}$$

and

$$p(x) = \frac{\alpha_1 x}{\alpha_1 x + \alpha_2(1 - x)}.$$

Now  $E\hat{\alpha}_1 = E\phi_x(P_1)$  and so

$$\frac{d}{dx} E\hat{\alpha}_1 = \sum_{j=0}^m \left[ \frac{\partial}{\partial x} \phi_x \left( \frac{j}{m} \right) \right] p(j, x) + \phi_x \left( \frac{j}{m} \right) \frac{\partial}{\partial x} p(j, x) \quad (\text{A9})$$

At  $x = \frac{1}{2}$ ,  $\phi_x(P_1) = P_1$  and  $(\partial/\partial x)\phi_x(P_1) = -4P_1(1 - P_1)$ . Thus (A9) reduces to

$$-4EP_1(1 - P_1) + \left. \frac{\partial}{\partial x} EP_1 \right|_{x=1/2} = \frac{4\alpha_1\alpha_2}{m}.$$

## ACKNOWLEDGMENTS

I am indebted to William Murdoch and Jean Chesson who gave me their raw data. Discussions with William Murdoch, Peter Abrams, and Jean Chesson, and the comments of Simon Levin and an anonymous reviewer, have been very helpful. This work was supported in part by an Australian CSIRO postdoctoral studentship and NSF Grant DEB79-22131.

## REFERENCES

- CHESSON, J. 1978. Measuring preference in selective predation, *Ecology* **59**, 211–215.
- CHESSON, J. 1983. The estimation and analysis of preference and its relationship to foraging models, *Ecology* **64**, 1297–1304.
- CHESSON, P. L. 1978. Predator-prey theory and variability, *Ann. Rev. Ecol. Syst.* **9**, 323–347.
- CHESSON, P. L. 1981. Models for spatially distributed populations: The effect of within-patch variability, *Theor. Pop. Biol.* **19**, 288–325.
- CHESSON, P. L., AND WARNER, R. R. 1981. Environmental variability promotes coexistence in lottery competitive systems, *Amer. Natur.* **117**, 923–943.
- COX, D. R., AND HINKLEY, D. V. 1974. "Theoretical Statistics, Chapman & Hall, London.
- JOHNSON, N. L., AND KOTZ, S. 1970. "Distributions in Statistics: Continuous Distributions, 2," Wiley, New York.
- McNAIR, J. N. 1980. A stochastic foraging model with predator training effects: I. Functional response, switching and run lengths, *Theor. Pop. Biol.* **17**, 141–166.
- MANLY, B. F. J. 1974. A model for certain types of selection experiments, *Biometrics* **39**, 281–294.
- MURDOCH, W. W. 1969. Switching in general predators; experiments on predator specificity and stability of prey populations, *Ecol. Monogr.* **39**, 335–354.
- MURDOCH, W. W. 1977. Stabilising effects of spatial heterogeneity in predator-prey systems, *Theor. Pop. Biol.* **11**, 252–273.
- MURDOCH, W. W., AVERY, S. L., AND SMYTH, M. E. B. 1975. Switching in predatory fish, *Ecology* **56**, 1094–1105.
- MURDOCH, W. W., AND OATEN, A. 1975. Predation and population stability, *Advan. Ecol. Res.* **9**, 1–131.
- OATEN, A. 1977. Optimal foraging in patches: A case for stochasticity, *Theor. Pop. Biol.* **12**, 263–285.
- OATEN, A., AND MURDOCH, W. W. 1975. Switching, functional response and stability in predator-prey systems, *Amer. Natur.* **109**, 299–318.
- REAL, L. A. 1977. The kinetics of functional response, *Amer. Natur.* **111**, 289–300.
- REED, R. C. 1971. "An Experimental Study of Prey Selection and Regulatory Capacity of the Bluegill Sunfish (*Lepomis macrochirus*)," M. A. Thesis, University of California, Santa Barbara.
- TANSKY, M. 1978. Switching effect in prey-predator system, *J. Theor. Biol.* **70**, 263–271.