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ABSTRACT

Generalist predators are typically considered to eat foods in proportion to their availability. I show that striped skunks, archtypal generalists, do not just eat foods as available, do not even just select for foods, but switch selection among prey types. In various experiments I showed that skunks do not change prey preference, but they do change preference for where they look for prey, they learn what types of microhabitats prey are found in, they form olfactory search images of prey (OSI), they form these OSI both in the short term and in the long term, both for many small prey items and for few large ones, they form OSI's in relation to what habitat the skunks are searching in, and they change foraging pattern in response to finding different types of foods.

Many other predators use one or other of these mechanisms, but rarely has an animal been shown to use several - I argue that this is because biologists have not looked for many such mechanisms together, and that it is common for generalist predators to switch among prey types. If it is common, then generalist predators should exert density-dependent predation on prey, and should to some extent, regulate prey densities. I discuss various field studies of predator-prey relationships that suggest this.

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1. INTRODUCTION

From the first studies of population biology to the present, biologists have not even agreed on what factors affect numbers of animals. Many factors, such as food supply and self-limitation, are difficult to study because their effects are not always obvious. For example, it is hard to tell if in nature the lack of food causes animals to bear fewer young. However, predation is more obvious; when an animal is eaten by a predator, it is dead, and numbers go down by one.

Despite this, from early studies to the present, biologists have not even agreed on whether predators affect prey numbers. Of the early population biologists, Leopold (1933) included predation as a limiting factor on animal numbers, but Elton (1942) concluded that "...we can see that there are inherent properties of the population dynamics of voles...that are not so much dependent on other animals like predators and parasites as we at first supposed." Chitty (1957, p 277), a student of Elton, said that "it seemed more or less certain that the following factors could be eliminated as sufficient causes of this type of population decrease:...predation...".

Currently there is still no agreement. Sih et al. (1985: p 283) reviewed some of the literature on predation and suggested that "Almost all of the studies showed some significant effects [of predation], and the great majority showed some large effects", yet Kuno (1987: p 328) also reviewed the subject and concluded that "the relative role being played by predators as the regulator of animal populations is negligible or subsidiary, at best, in natural ecosystems."

One of the problems is that often field studies have not differentiated between specialist and generalist predators (by this I mean predators feeding on one versus many prey types). The two can affect prey populations in very different ways.

It is especially important to know how generalists react to different prey - they are usually thought to feed on whatever prey are available (without selecting for any one prey type), but this is not often the case. In order to see how generalists can stabilize prey numbers, and how often this happens in nature, we can first narrow the range of mechanisms we consider by seeing what theoretically stabilizes and destabilizes populations.

In the 1920's Lotka (1925, cited in Krebs 1985) and Volterra (1928, cited in Taylor 1984) showed that model predator-prey populations oscillated. Although the assumptions and behavior of the model were unrealistic, biologists embraced it; it was the first good explanation for the cycles in animal populations that people had observed in nature (Murdoch and Oaten 1975).

The Lotka-Volterra model assumes that prey numbers grow exponentially and that each predator eats a certain constant proportion of prey. It also assumes that predators die exponentially, but that their numbers grow linearly with the number of prey eaten. It is a differential equation model, which implies that all effects occur instantaneously. Obviously, these assumptions are unrealistic; in nature, prey have upper limits to growth, predators get satiated and animal populations do not respond instantaneously to changes in conditions.

Because of these unrealistic assumptions, the model acts unrealistically, behaving with "pathological dynamic" properties (May 1976: p 50). The populations cycle at whatever amplitude they initially started, and any deviations from the assumptions tip the system into stability or instability. However, even though the model is unrealistic, this knife-edge neutral stability is very useful since one can add various realistic features to see if they push the system into stability or instability (Murdoch and Oaten 1975).

Theoretical predator-prey systems are stabilized by prey population growth

limits (May 1973), by density-dependent predation rates, by rapid growth rates of predator populations relative to prey populations (Taylor 1984), and by a fast response of predators to changes in prey density (short time lags; Murdoch and Oaten 1975). Although growth limits to prey can stabilize the predator-prey system, this has nothing to do with predators. When prey by themselves are stable, then prey and predators together are more likely to be stable (May 1973).

Density-dependent predation occurs when predation rate increases in response to an increase in prey density. Note that it is not only that number of prey killed increases, but that proportion of prey killed increases. This can occur as follows (Solomon 1949): first, predator numbers can increase (this is called the numerical response), and second, predators can increase the numbers of prey killed by each predator (this is called the functional response). The two responses together give the total change in predation rate.

Theoretically, the faster that predator populations grow when prey numbers are high, the more stable the interaction. Tanner (1975) showed that of 8 natural predator-prey systems, the only one (hare-lynx) that cycles (i.e. is unstable) is the only one with a low population growth rate of predators relative to prey and a high prey carrying capacity.

However, in nature, the numerical response of generalists rarely stabilizes a system. If one type of prey doubles in density, the food supply of a specialist doubles, but that of a generalist increases much less. Therefore, the population size of the generalist responds much less to such an increase in food supply than that of the specialist. Furthermore, predator populations rarely grow even as fast as prey populations; predator reproduction is restricted by how much of the prey production they consume and by how efficiently they turn that consumption into reproduction.

In addition, predator numbers do not respond instantaneously to a rise in

prey numbers; there is usually a time lag, which will destabilize the system (Murdoch and Oaten 1975). Most animals have discrete breeding seasons and thus birth rate does not change immediately after a change in the environment; effects are not felt instantaneously. Predator numbers overshoot and undershoot, leading to cycles. The larger the time between breeding seasons, the more unstable the system.

On the other hand, some kinds of functional responses lead to stability. Holling (1959a, 1959b 1961, 1965) described three different types of functional responses. Type I is a linear response of numbers of prey killed per time per individual predator versus prey density - each predator eats a constant proportion of prey. This is what the Lotka-Volterra model assumes, and is unrealistic because predators normally become satiated. Type II is an asymptotic response - it represents gradual predator satiation. Type III is a sigmoidal response - predators switch on to prey, then get satiated.

The specific form of the functional response determines how it affects stability - if proportional predation rate increases when prey density increases, then the system will tend to stabilize (Taylor 1984). In the type I functional response, predation rate is constant, causing the neutral stability of the basic Lotka-Volterra model. In type II, predation rate decreases with prey density, causing destabilization. In type III, predation rate first increases and then decreases, leading to stabilization at lower prey densities and destabilization at higher prey densities. If prey numbers can reach high enough levels, they escape regulation by predators. The type III functional response is the only one that may lead to population regulation by predators.

Although a type III functional response can theoretically stabilize prey numbers, we cannot assume that it does so in nature. Very few predators have been shown to have a type III functional response with one prey type. It is difficult even to

think of mechanisms that would cause specialists to accelerate their response to prey. Murdoch and Oaten (1975: p38) reviewed the literature and concluded that "... type 2 curves seem to be the rule among predators feeding upon one species of prey." This result applies to such a wide range of organisms that one might suspect it is the basic and most widespread response."

However, adding more prey species adds another way to get a type III response: when density of one prey type is high, the predator could select for that prey; when density is low, the predator could select for others. This is called switching (Murdoch 1969). Switching does not just mean that predators change how many prey they eat, but that they change actual selection*. The additional prey species create a greater potential range of prey densities over which density-dependent predation can act, and thus a greater stabilizing effect. With only one kind of prey, a predator must eat a minimum number of that kind to stay alive; but with more than one kind, a predator can eat none of that type by switching on to others. With one prey type, the bounds of density-dependent predation are determined by satiation and starvation; with several prey types, the bounds are determined by satiation and zero prey. Therefore, generalists can stabilize prey populations by switching.

For a predator to switch prey, it must change selection when a given prey increases in density. It is not necessary to change from selection against that prey to

*The words 'selection' and 'preference' are often used in different ways. I will use them as follows: selection is when predators eat prey in different proportions to those found in the environment; preference occurs when predators select prey even when prey are encountered and detected equally. Preference is thus one way to select for prey, but there are others. For example, a predator may search in certain microhabitats, and thus catch some prey more than others.

selection for it; selection for that prey must simply increase. For example, suppose a predator selects strongly against a prey at low prey densities, and less strongly against it at higher prey densities. From the prey's point of view, predation rate increases when prey density increases, irrespective of the fact that the predator is still catching it at a lower rate than it is catching other prey.

If we consider a sequence of prey captures, switching occurs if and only if catching one type of prey increases the chance that it will be caught again in the near future. Then, when a prey population increases in relative density, by chance that prey is caught more often, leading to a greater chance that it is caught again, leading to increased selection. Therefore, in order to show that a predator switches prey, we have to show either that 1) catching an individual of one prey type increases the chance it will be caught again in the near future, or 2) the proportion of prey caught increases more than an increase in relative prey density.

Although it has been shown that many animals possess a mechanism for switching, rarely have generalist predators been shown to possess more than one switching mechanism. In this study, I tested for several mechanisms of prey switching by the striped skunk (*Mephitis mephitis*), in the belief that if this classic generalist predator can easily switch among prey by using several different mechanisms, then it is likely that many other generalists can as well.

To tease apart what kinds of behaviors cause switching, I considered the predatory sequence. First a predator must decide where to look for prey, then must detect prey, and finally must capture it. In particular, I studied the short-range aspects of foraging - what skunks do once they are in the vicinity of prey. I examined prey preference (choosing to pursue prey), microhabitat learning (learning where prey are found), search image formation (detecting prey) and foraging pattern (how to search for prey) by conducting two different types of experiments: 1) skunks were

presented with a sequence of prey items, and 2) skunks were presented with different densities of prey items (see Fig 1 for a flow chart of the experiments).

2. DESCRIPTION OF STUDY ANIMALS

Skunks generally live everywhere within their geographic range, preferring open or forest edge areas (especially agricultural areas) (Hamilton and Whitaker 1979), but not unbroken forested areas (Verts 1967). Within their home ranges, they concentrate feeding in certain habitats during different times of the year (Crabtree 1984, Sargeant pers. comm., Nams pers. obs). Within one night, they may feed in one small area for several hours, then move to another area (Sargeant pers. comm., Nams pers. obs.).

The distance that skunks move depends on age, sex and time of year. In the fall, juveniles disperse from several to tens of kilometers from the parent home range (Verts 1967, Bailey 1971, Bjorge et al. 1981). During the spring and summer, males use slightly larger home ranges than females (home ranges vary from 2.2 to 5 km² in rural areas; Storm 1977, Bjorge et al. 1981, Rosatte and Gunson 1984). Females use one den site for up to several weeks when they are raising young, but males and females at other times of the year may use the same den for only one to several days in a row (Rosatte 1985, Nams pers. obs.). Therefore, skunks are sometimes central-place foragers, in that they return to the same spot after foraging (Rosatte 1985), and sometimes they are not. Skunks do not defend territories and there is much overlap of individual home ranges.

Figure 1. Experimental design. Boxes refer to experiments.

WHAT PREY TO CHOOSE

Prey preference

Preference
ChamberWHERE TO SEARCH FOR PREY

Side preference

Learning types of places

HOW TO DETECT PREY: OLFACTORY SEARCH IMAGEShort Term

Reaction to one prey type

Reaction to prey using two senses

Reaction to two prey types
within one senseLong TermHow search image changes
from day-to-dayForm search image with only
one large item per dayInteraction

Search image x habitat interaction

HOW TO SEARCH FOR PREY

Foraging pattern

Skunks use different methods to find different types of food. They smell and dig out underground insects, they walk along and pounce on grasshoppers and ground beetles, they find nests by smell, and they sit and wait to ambush small mammals (Crabtree 1984, Rosatte 1985, Sargeant pers. comm., Nams pers. obs).

I chose to study striped skunks both because they are considered to be opportunistic omnivorous predatory feeders (Carr 1974) and because they are very easy mammalian predators to work with. Although they eat many different kinds of foods, their diet is not the same year-round: in the spring skunks eat more birds' eggs, in the summer more insects, and in the fall more small mammals and vegetation (Hamilton 1936, Selko 1937, Verts 1967). These are only general trends - at all times of the year they eat many types of foods. Rosatte (1985) considered skunks' feeding pattern to be one of eating mostly insects, but shifting their diet to small mammals, birds' eggs, birds and vegetation when insects are not available (spring and fall). No one has measured prey selection to show how dependent these diet shifts are on prey availability. The general impression is of an animal that eats whatever it finds.

The first suggestion that skunks are not typical non-switching generalists was made by Crabtree (1984). He noticed that skunk predation on duck nests declined after spring, and suggested that skunks changed from actively seeking nests to a sit-and-wait mode of feeding on small mammals and insects when they became more numerous. Skunks may have switched from nests to other prey.

3. GENERAL METHODS

To capture wild skunk kittens, I disturbed the den site of a lactating, radio-collared female. When the female moved her young from the den site, I netted three kittens (one male and two females). The kittens were likely 6-8 wk old when

captured, since I was able to wean them the following week (wild skunks usually are weaned at 6-8 weeks; Verts 1967). I immediately descended the kittens (following methods of Fowler (1978) and Wilbee (pers. comm.)), and began behavioral experiments with them in 1985.

The skunks were housed in mesh cages (1.5 x 1 x 1 m), each with a wooden nest box (30 x 30 x 30 cm) and a litter box. They had free run of a 2m x 4m indoor area and spent many of their waking hours running on a large exercise wheel. Due to behavioral problems (fights in autumn, mating fights in spring), I occasionally separated the skunks. At such times I alternately kept one or two in cages while the other(s) ran free. The skunks were fed dry kibble dogfood and occasional table scraps.

After familiarizing the skunks with collars, I gradually trained them to walk outdoors on a leash (a light 4m string). I could never pull them along, as with a dog, but could only stop them from going in a certain direction by holding the leash tight. During the experiments I used the leash to 1) ensure that the skunks would not escape if they were frightened (e.g. they ran if they heard a vehicle), 2) stop them from straying off the study area, and 3) guide them in certain directions by stopping them whenever they went in the 'wrong' direction. Although the skunks were tame enough to ignore me while foraging (I could peer at them from a distance of 30cm, apparently without disturbing them), they did not like to be touched or picked up, and were usually frightened of strangers. When outdoors, I never fed the skunks by hand; thus, they never associated people with food while outdoors.

I carried the skunks to different study areas in three separate carrying boxes strapped to a packframe. I enticed them into the boxes with food, although at the end of an experimental session they often entered voluntarily.

3.1 SAMPLE SIZE

The major flaw in the methods is the small sample size - for all of my experiments I used three individual skunks. However, I think the results are still valid because I am asking very general behavioral questions - that is, do certain behaviors exist - not measuring specific parameters. For example, if three skunks can form search images, then it is likely that most skunks can. On the other hand, more quantitative questions are different; for example, measuring consumption rates would require many individuals. The important thing is whether inter-individual variability is the same as or greater than intra-individual variability. In almost all of my experiments the two were similar.

More important, this study would have been impossible to do with many more than three animals - rearing, training, and working with even three required a great deal of time and energy.

These types of questions that require in depth experiments typically are answered with few experimental animals. For example, Pietrewicz and Kamil (1979) used five individuals to show that blue jays form search images; Davis (1984) used one individual to show that raccoons can discriminate the number 3; Bond (1983) used three individuals to show that pigeons cue in to foods visually; and MacDonald (1976) used one individual to show that foxes can remember where they cache food.

4. GENERAL ANALYSIS

For each experiment I did a series of trials with each animal and analyzed the results obtained as follows. If there were no significant differences among animals, I combined data from all animals and did statistical tests on the combined data. If there were significant differences among animals, I then analyzed the data from each animal separately and presented the results separately. This was an

attempt to solve the problem of repeated measurements on the same individual; that is, one that assumes within-individual variation is a good estimate of among-individual (population) variation, which is often not the case. I combined data for all individuals only if there were no significant differences among animals; i.e. within-individual variation was not greater than among-individual variation.

Whenever I combined estimates and variances of some parameter either over all individual animals, or over replicates of some treatment, I estimated a variance of the overall mean. To do this, I first tested for significant differences among groups (using an ANOVA). If there were differences, then for the variance of the overall mean I used the variance estimated among the individual parameters (ignoring each of their associated variances). If there were no differences among groups, I then used an estimate of variance which treated all data as belonging to one large sample combined (see Appendix 1 for explanation).

Often the parameters I used had very different variance estimates, and thus a standard ANOVA was not valid. In this case I used a weighted ANOVA and weighted parameter estimates, weighting the parameters by the inverse of their variances (Searle 1971, Cochran 1977). On one hand the weighted ANOVA removes the problem of heterogeneous variances, but on the other hand it gives an incorrect value for degrees of freedom. However, I compared the results of each weighted ANOVA to an unweighted one and found that they almost always agreed on significance.

5. EXPERIMENTS

5.1 PREY PREFERENCE

The most obvious way for predators to change prey selection is actually to change what types of prey they choose - that is, to change prey preference. So, I

tested to see if prey preference of skunks was dependent on past diet. I did this by offering the skunks pairs of similarly-preferred food items simultaneously and seeing if they preferred the type of food they had eaten in the past. Since animals are more likely to reveal a preference when foods are offered simultaneously than when they are offered sequentially, and are also more likely to switch between similarly preferred foods than between very different ones (Curio 1976), this technique is a liberal test of switching in prey preference - it will err on the side of showing a change in preference.

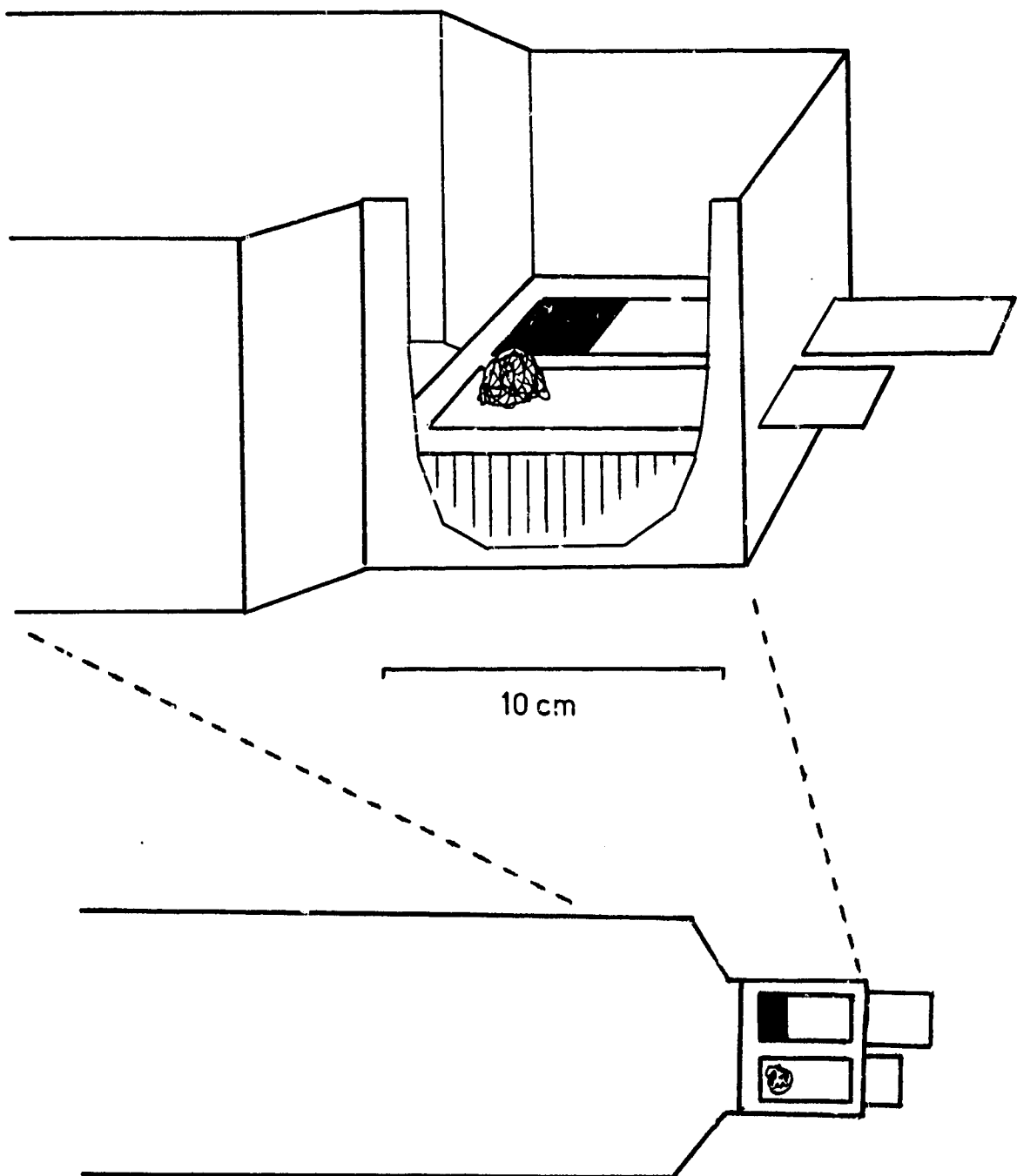
5.1.1 Methods

I used a test chamber that allowed skunks to see and smell two food items simultaneously, but eat only one (Fig 2). The chamber was open at the top and at one end, and the food was presented at the closed end. The chamber was about 60 cm long and 20 cm wide in the main section and 10 cm wide at the food end. The narrower section at the food end forced the skunks to approach the food head on, rather than from one side or the other. Thus they would see and smell both food items at the same time. When the animals took a food item, I pulled out the door under the other one, dropping it out of sight. Thus they could eat only one food item. I habituated the skunks to this chamber with food for several days before the actual experiments.

Food items used were 1 gram pieces of raw ground meat and various flavors of canned cat and dog food. The size of the pieces simulated such small natural food items as insects. The skunks generally preferred these test foods over dry dogfood (their usual diet). For each experiment, I used the same two types of food during a feeding session, but varied food among feeding sessions. Thus the experiments tested for changes in preference in general, not just between two types of food. In all

Figure 2. Prey preference chamber, set up to allow skunks to see and smell two food items simultaneously, but eat only one. Top part of figure shows view from side of chamber and bottom part of figure shows view from top of chamber.

Two pieces of food were placed at the right end and the skunk entered at the left end. When the skunk took a piece of food, the door under the other piece was pulled out, dropping it out of reach.



experiments I kept food type and side (left/right) independent so that any inherent preference for side did not affect prey preference.

I did a series of five experiments (Fig 3), in each of which I estimated the probability that food type eaten was same as eaten in the past. The first experiment tested for a general switching in prey preference, whereas experiments 2 - 5 tested for effects of different amounts of experience on switching in prey preference.

Experiment 1 tested whether eating a given type of food in the past generally affects prey choice in the future. In each trial I offered the skunks a series of choices between two types of food and for each choice noted whether food type eaten was the same as or different from the previous one eaten. This experiment measured the general effect of past experience, not a specific amount of past experience. If switching occurred, it would lead to the animals eating foods in runs. For example, if a skunk ate food1, it would more likely eat food1 next time. If it did eat food1 next time, it would even more likely eat it again. Thus the skunk would eat food1 several times consecutively (and similarly for the other food item).

I counted how often food type eaten was the same as or different from the previous one eaten. If skunks ate food items in runs, then food eaten would more likely be the same type as the previous one eaten. If skunks ate food items randomly, then food eaten would be independent of the previous one eaten. If skunks tended to alternate food items, then food eaten would tend to be different from the previous one eaten. Testing for a positive relationship between previous and present food eaten is equivalent to testing for runs (and switching).

Experiments 2 to 4 tested whether eating a type of food a certain number (2, 10 and 40) of times consecutively is sufficient to determine prey preference. For each experiment I did a sequence of trials using 2 foods (food1 and food2). In each trial, I first offered the skunks n choices between one of the foods and another food

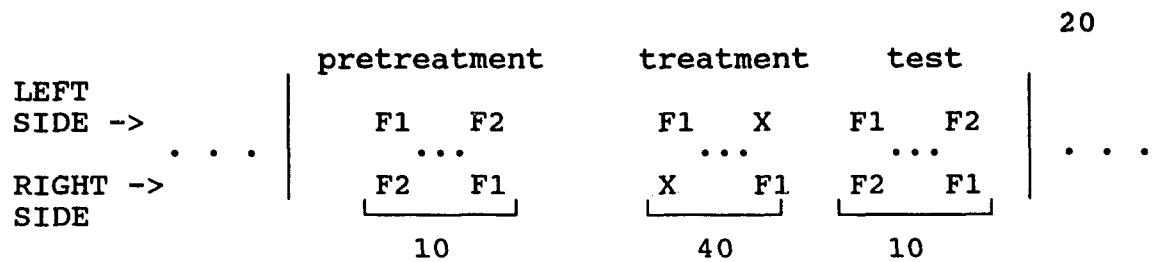
Figure 3. Design of prey preference experiments. F1 and F2 refer to the two types of foods used in the test sections. X refers to unpreferred food (dogfood kibble) used in the treatment sections to ensure that skunks eat the other type of food.

LEFT SIDE -> . . . F1 F2 F2 F2 F1 F2 F1 F2 . . .
 RIGHT SIDE -> F2 F1 F1 F1 F2 F1 F2 F1
 one trial

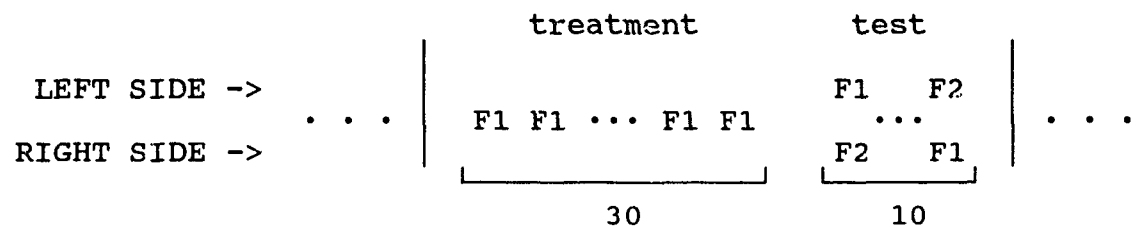
EXPERIMENT 1. Tested for general effect of past prey eaten on prey preference.
 A series of offerings (trials) of food1 (F1) and food2 (F2), on random sides.

		treatment	test	
LEFT SIDE ->	. . .	F1 X	F1	. . .
RIGHT SIDE ->		<u>X F1</u>	<u>F2</u>	
		2	1	
		one trial		

EXPERIMENTS 2 & 3. Tested for effects of 2 and 10 food items eaten in the past, on prey preference. For experiment 2, in treatment section, attempted to entrain skunks to food type by offering two choices between food1 and nonpreferred food X (always kibble dogfood). In test section, measured preference for food1 versus food2 by offering one choice. Repeated whole procedure, but using food not chosen in previous test section in next treatment section. Randomized offerings on right vs left sides. For experiment 3, used 10 and 6 instead of 2 and 1 to see what effect more exposure to food has on preference.



EXPERIMENT 4. Tested for effects of 40 food items eaten in the past, on prey preference. In pretreatment section, measured preference between two foods. Then, using F1 for the food selected against, followed format for experiments 2 & 3, but used 40 and 10 in the treatment and test sections. Repeated next day.



EXPERIMENT 5. Tested for effects of 30 food items eaten in the past, on prey preference. In treatment section, attempted to entrain skunks to food type by offering 30 pieces of food1. In test section, measured preference for food1 versus food2 by offering 10 choices. Repeated next day, using the food not chosen in the previous test section in the next treatment section.

(Figure 3 continued)

they rarely chose, then offered a choice between foods 1 and 2 m times consecutively. In the first part of the trial I used the food they had not chosen in the previous trial. I attempted to habituate the skunks to this food by only offering choices between that food and dry dogfood (they rarely chose the dogfood). These trials were repeated many times. Experiments 2 and 3 used (n,m) values of $(2,1)$ and $(10,6)$, respectively.

Because of satiation, the procedure in experiment 4 (with n,m of $40,10$) was slightly different. Only one trial was done per day. First, to find what food skunks did not prefer, I offered them 10 choices between food1 and food2. Then to habituate them, I let them eat 40 items of the food type selected against. Finally, to test for preference, I again offered them 10 choices between food1 and food2.

Note that in experiments 2 to 4 the treatment food type was always the one that was not preferred before the treatment. This ensured that if skunks chose the same food in the test section as the treatment section, this happened because of the treatment, not simply because they had previously preferred that food. Thus these experiments measured whether n items of food were sufficient to determine or affect preference, irrespective of any previous preference.

Experiment 5 tested, in a different way, whether eating a type of food 30 times consecutively is sufficient to affect prey preference. I offered skunks 30 pieces of only one type of food (food1 or food2) and let them eat it all. In contrast to the other experiments, the skunks had no choice. Then the skunks were tested with 10 choices between food1 and food2. Trials were not repeated the same day because of satiation.

5.1.2 Analysis and Results

For each experiment I estimated the probability that a certain type of prey is chosen, given it was eaten n times previously and that it was not preferred before

that. This was $P = x/(x+y)$, where x = number of times the treatment series food was chosen in the test series, and y = number of times the other food was chosen in the test series. A probability greater than 0.5 means that prey preference switched - that there is greater than 50% chance that skunks eat the type of prey recently eaten. I used a normal approximation to the binomial distribution to estimate confidence intervals for P .

Note that when $P = 0.5$, skunks eat both foods, sometimes eating one and sometimes the other. This does not mean they switch prey preference. 'Switching' in reference to a change in prey preference does not mean the same as 'switching' in reference to changing back and forth in time between different prey. Switching preference means that an animal prefers one prey type more as that prey becomes more numerous, and prefers it less as that prey becomes less numerous. This happens because the prey is encountered more often as it becomes more numerous, and as it is encountered more often, the predator starts to choose it over others. The predator tends to choose the prey that it has recently fed upon. If the predator simply alternates randomly between two types of food, then when one prey becomes more numerous, the predator prefers it the same amount as before.

Individual skunks changed prey preference in a similar way in each of the 5 experiments (Table 1), and so I combined data from all individuals. In each experiment, skunks chose foods independently of the previous ones eaten (Table 1). However, for some of the experiments, the 95% confidence interval for P is quite large; therefore these experiments are not very precise tests for a change in prey preference. There might be small effects that they cannot measure.

The confidence interval for P can be decreased by combining results from all experiments - this measures the general effect of previous foods on food choice. There is no difference among experiments in the effect of previous foods on food

TABLE 1. Effects of previous experience on prey preference. Overall, skunks did not change prey preference as a result of previous experience, and there were no differences among individual skunks. Skunks switch if $P > 0.5$. P is the probability (+ 95% confidence interval) of choosing the same type of prey as previously eaten during n previous food items. N is the total number of test trials. 'Differences Among Individuals' are results of chi-square tests among individual skunks.

Expt.	Probability (P)		n	N	Differences Among Individuals	
					χ^2	D.F
1	0.44	(± 0.06)	1	214	2.2	2
2	0.50	(± 0.16)	2	40	0	1
3	0.49	(± 0.09)	10	118	3.5	2
4	0.41	(± 0.19)	40	29	2.26	1
5	0.44	(± 0.19)	30	23	0.03	1
COMBINED	0.46	± 0.05		424		

choice (X^2 among experiments = 0.84, d.f. = 4), and so I combined their results for a general measure of switching of prey preference. I did this by summing frequencies of the number of same and different foods eaten for all experiments, and estimating the general probability and confidence intervals. The combined probability is thus a weighted mean (weighted by sample sizes) of the individual probabilities.

The combined P is a measure of the probability that a certain food will be chosen, given that it has been eaten more than the other one during the same feeding session. For these experiments, the combined P ($0.46 \pm 0.05^*$; Table 1) is not significantly different from 0.5, even though it is a more precise estimate than for the individual experiments. This means that skunks choose food independently of their recent experience. Skunks do not switch foods by switching prey preference during a feeding session. Note that this does not mean that skunks do not prefer foods, but that they do not change preference.

5.2 SIDE PREFERENCE

In the prey preference experiments, food type was kept independent of side type; thus any preferences for side would not affect prey preference measurements. However, skunks did prefer sides, and this preference was not constant. Perhaps skunks change side preference as a result of recently eating prey from a particular side. If so, then I interpret this to mean that skunks choose where to look for prey. On the other hand, if simply a side preference forms that is not dependent on past experience, then some outside factor may be causing this bias.

*Whenever I present estimates of parameters, I present the estimate along with + 95% confidence intervals.

5.2.1 Methods

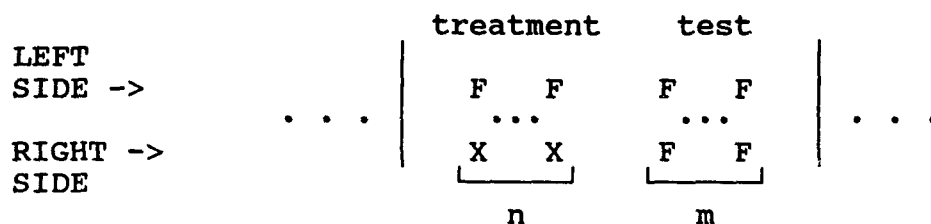
I first tested to see if skunks change preference for sides, and then in the following experiments, I measured how much previous experience was needed to affect side choice. These experiments used the prey preference chamber and were set up similarly to the prey choice experiments. In some of the experiments I used only two animals because one was injured.

To see if skunks change preference for sides, I analyzed the data from the first prey preference experiment for changes in side choice instead of prey choice (I will call this the first experiment for this section, even though it is the same one as the previous section). In that experiment I presented skunks with a sequence of choices between two foods, keeping food type and side type independent. I tested for independence between last side choice and next side choice.

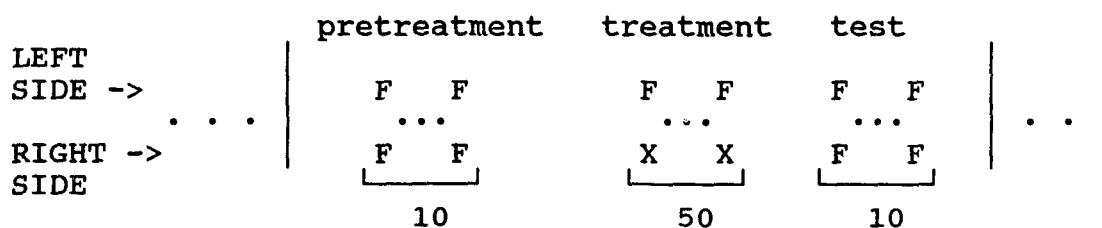
Experiments 2 to 5 tested whether eating food from a specific side a certain number of times is sufficient to determine side choice (Fig 4). First, in an attempt to habituate the skunks, I let them eat n times food from whichever side they had not chosen in the previous trial. I did this by offering choices between food that they preferred and food that they did not prefer (dry dogfood). Then I tested side preference by offering them a series of m choices between two pieces of the same type of food. This procedure was repeated many times. Experiments 2,3,4 and 5 consisted of (n,m) values of (2,1), (5,5), (10,5-10) and (50,10), respectively.

Because of satiation, the procedure in experiment 4 (with n,m of 50,10) was slightly different. Only one trial was done per day. First, to find what side skunks did not prefer, I offered them 10 choices between two pieces of the same type of food. Then to habituate them, I let them eat 50 times food from the side selected against. Finally, to test for side preference, I again offered them 10 choices between two pieces of the same type of food.

Figure 4. Design of side preference experiments. F refers to the food used in the test sections. X refers to unpreferred food (dogfood kibble) used in the treatment sections to ensure that skunks eat food from a certain side.



EXPERIMENTS 1 - 4. Tested for effects of various amounts of experience (n) in the past, on side choice. In treatment section, attempted to habituate skunks to side type by offering n choices between preferred (F) and nonpreferred (X) food, keeping F on one side only. In test section, measured preference for left or right side by offering m choices between F on two sides. Repeated whole procedure, but using side not chosen in previous test section in next treatment section. Experiments 1 - 4 used different n,m values.



EXPERIMENT 5. Tested for effects of eating 50 prey items from a certain side in the past, on side choice. In pretreatment section, measured preference for side. Then followed format for experiments 1 - 4. Repeated next day.

Note that the treatment side was always the one that was not preferred before the treatment. This ensured that if skunks chose the same side in the test section as the treatment section this happened because of the treatment, not simply because they had previously preferred that side. Thus these experiments measured if n choices were sufficient to determine or affect preference, irrespective of any previous preference.

5.2.2 Analysis and Results

The data were analyzed as in the prey preference experiments. P measures the probability that a certain side is chosen, given it was chosen n times before and was not chosen before those n times. A probability greater than 0.5 means that side preference changed - that there is greater than 50% chance that skunks eat food from the same side as previously.

Individual skunks differed significantly in how readily they changed side preference for n of 2, 10 and 50 (Table 2). Thus I could combine data for all individuals only for experiments 1 and 3.

Previous side chosen did affect next side choice (Table 2) overall. I interpret this to mean that skunks learn where to find food. The pieces of food were spaced so close (about 1 cm) that skunks would see both at once. If skunks learn where to find food when there is such a small difference in locations, then they should be even more likely to learn where to find food in the wild, where differences are greater.

The probability of choosing the same side as in the n treatment choices generally increased as n increased (Table 2), and between n of 10 and 50 the probability passes 0.5. In fact, for $n = 2$, the animals are more likely to choose the opposite side. This does not necessarily mean that after choosing a side twice consecutively skunks will choose the opposite side next, but possibly that two treatment choices were not enough to 'unlearn' the initial side preference. The side

TABLE 2. Side choice: effects of previous experience during the same day on side preference. Skunks changed side preference in experiments 1 & 5. P is the probability (+ 95% c. i.) of choosing food from the same side as during n previous choices. N is the total number of test trials. Probability values are also shown for individual animals whenever animals differ. 'Differences Among Individuals' are results of chi-square tests among individual skunks.

Expt.	Animal	Individual Probability		n	N	Differences Among Individuals	
		(P)				χ^2	D.F
1		0.65	(± 0.06)*		232	4.9	2
2		0.41	(± 0.11)	2	74	5.9#	1@
	1	0.54	(± 0.15)		43		
	2	0.23	(± 0.15)*		31		
3		0.57	(± 0.12)	5	60	0.30	2
4		0.53	(± 0.09)	10	111	6.1#	2
	1	0.43	(± 0.14)		51		
	2	0.66	(± 0.13)*		50		
	3	0.40	large		10		
5		0.89	(± 0.05)*	50	164	13.0#	1@
	1	1.0	(0.95-1.0)*&		72		
	2	0.80	(± 0.08)*		92		

P significantly different from 0.5 at $p < 0.05$.

* Significant at $p < 0.05$.

@ All d.f. = 1 tests used correction for continuity.

& Used non-normal c. i., because P is close to 1

used as the treatment side was always the one that had not been preferred in the previous test. Thus the experiments tested to see if n trials were sufficient to determine side choice.

Fifty choices are sufficient for skunks to learn where to find food. Usually the animals were satiated after a test of $n = 50$, so this can be thought to represent one feeding session on small items, such as insects, in the wild. Thus one feeding session is enough for skunks to learn where to find food.

If it takes almost a whole feeding session to learn where to find food, skunks will benefit little from this unless they remember from one feeding session to the next. To see if skunks remember side choice from one feeding session to the next, I re-analyzed data from experiment 5. I compared side choice from the end of one day to the start of the next day, to see if, at the start of the next day, the same side was chosen as the previous day. Although an inherent, constant side preference would also give significant results, the skunks did change side preference from the beginning to the end of each session during each day of the experiment (probability of changing side preference = 0.89; Table 2). Therefore this comparison only measured remembering from one day to the next.

The two individuals tested remembered significantly different amounts, but each one did choose the same side as the previous day more frequently than the other side (Table 3). Skunks learn where prey are found during one feeding session, and remember from one feeding session to the next.

5.3 LEARNING TYPES OF PLACES

The above experiments showed that skunks tend to choose food from the side where they previously ate their preferred food. However, I forced the skunks to eat from a specific side in the treatment sections by offering them a choice between a preferred and a nonpreferred food. The effect is so strong that, after the skunks

TABLE 3. Side choice: effects of experience during the previous day on side preference. Skunks did remember side preference from one day to the next. P is the probability (+ 95% confidence interval) of choosing food from the same side as the previous day . Probability values are also shown for individual animals, since they differ. N is the total number of test trials. 'Differences Among Individuals' are results of chi-square tests among individual skunks.

Individual Animal	Probability (P)		N	Differences Among Individuals	
				X2	D.F.
Both	0.77	(± 0.07)*	143	13.9	2
1	0.90	(± 0.07)*	71		
2	0.64	(± 0.11)*	72		

* Probability value is significantly different from 0.5 at $p < 0.05$

formed a preference, they chose the usually non-preferred food several times before eating the preferred food from the other side. Still, these experiments did not show that skunks learn where to find food they recently fed on, but that skunks learn where to find preferred food. That is, perhaps in the wild, skunks learn where to find food only if it is strongly preferred, but not otherwise. Such experiments are not sufficient to show that skunks can switch among prey by learning where to find food in general.

In this next series of experiments I asked whether skunks learn what kinds of places to find food in, and if so, whether they more often search in those places as the density of that food increases.

5.3.1 Methods

I hid food under two different types of containers: small rounded styrofoam bottoms from egg cartons (A) and black styrofoam cups (B). I chose these two so that there would be obvious differences between them: A was small and white, while B was large and black. I then let each animal walk around freely and search for the food, and I counted how frequently they investigated each of the two places. From these frequencies I estimated a measure of selection.

I placed 123 and 25 (the number I had available) of A and B upside-down on 7.5cm x 7.5cm squares of plywood. The food was placed on the plywood, under the containers. These were distributed approximately equidistantly (more regular than random) within a 14m² floor area; containers A were about 30 cm apart and containers B were about 70 cm apart. I tried to distribute them so that whenever a skunk looked around from any one place, both A and B would be in view.

I compared the effects of different food densities by varying the percent of food under each type of container. If skunks learn in what types of places to find food, then selection for A should increase when food density under A increases.

For food, I used 1-3 grams of any one of: different flavors of canned catfoods and dogfoods, dry dogfood, mashed boiled eggs or raw ground beef. The same food type was used in both types of places during any one experimental trial; this ensured that skunks chose places, not food. I varied the type of food from day to day.

During a trial, the skunks walked around, approached the containers, and sniffed them. If food was present, the skunks pushed the container aside and ate the food. Since the animals approached the containers even if there was no food under them, I assumed that they could not tell if they were empty or not before they approached them. Thus, one choice was defined as the skunk sniffing a container, whether there was food beneath or not; this choice measured where skunks looked for food, not whether skunks found and ate food.

The main sequence of trials simulated the effects of a change in density of one food type in one type of place, and used ratios of 0:1, 0.2:1, 0.4:1, and 1:1. These represent the ratio of the percent of A's that contained food to the percent of B's that contained food - for example, at 0.2:1, 25 out of 123 A's and 25 out of 25 B's were occupied. Note that the different experimental treatments were carried out randomly. That is, not in the order 0:1, 0.2:1, 0.4:1, and 1:1. This ensured that skunks did not simply learn over several sessions that container A contained food, but that they would have to learn in each session where food was located.

Each trial consisted of 150 - 200 choices, with 1 - 4 trials for each animal for each prey density.

In the different experimental trials I varied the density of food under the containers, but kept the numbers of each type of container constant. In this way I simulated the effects of changes in relative density of prey - in the wild, prey densities change, but numbers of available places remain constant.

I did two other types of trials. One measured the maximum possible selection

for place A; it used prey densities of 1:0 (food under only A). The other measured the effect of different densities of places; it used prey densities of 0:1, but with the containers at half the normal density (i.e. an overall area of 28 m² compared to the usual 14 m²).

5.3.2 Analysis and Results

I estimated selection of places by a variation of a prey preference measure. Ivlev (1961) proposed a statistic to measure prey preference, using the number of each of two prey types available and the number eaten. Cock (1978) concluded that Ivlev's measure was one of the few without major drawbacks. In this experiment, number of places present represents number of each prey type available and number selected of each type of place represents number of prey eaten. Ivlev's preference index for A is given by:

$$Pr_A = \frac{\frac{A}{B} - \frac{N_A}{N_B}}{\frac{A}{B} + \frac{N_A}{N_B}}$$

Where A = number of place A investigated

B = number of place B investigated

N_A = number of place A available

N_B = number of place B available

Pr_A varies from -1 to 1, so I transformed it as follows to vary from 0 to 1:

$$S_A = \frac{1}{2} (Pr + 1) \quad (1)$$

where S_A is my measure of selection.

Thus S_A is similar to the probability of choosing A if both A and B are

presented simultaneously. Similarly, S for B is $1 - S_A$. An S_A -value of 0.5 means that two types of places are investigated in the proportions expected from their availability - no selection occurs. An S_A -value of 0 means that only type B is selected, and an S_A -value of 1 means that only type A is selected. However S_A is not completely analogous to the probability of choosing type A, because Pr (and therefore S_A) is more sensitive to small preferences than to large ones (Cock 1978).

S_A is not distributed normally and there is no easy variance estimate. I used a jackknife technique (Appendix 2) to get normalized estimates for S_A and its variance in order to use them in parametric statistics.

Since each skunk selected similarly among replicates for each prey density (X^2 tests of independence of frequencies of choices), I combined frequencies over all replicates for each individual. With these combined data, for all prey densities, skunks selected places similarly (Table 4), so I combined data for all individuals. This gave overall frequencies of A and B selected, and thus an S_A -value and its variance, for each prey density (Table 4).

Skunks selected place A more with increasing prey density (regression analysis relating density of food under A to S_A : F regression = 26.1, d.f. = 1,7432, $p < 0.001$), from choosing A 32% of the time when food was found only under B, up to a maximum of equally choosing A and B when food was only found under A (Table 4). Skunks learn in which types of places to find prey, in this way switching to prey when density of that type increases. Also, skunks did not select differently for A when densities of the places themselves were 1/2 of the usual densities (Table 4). Within the range of densities of these trials, place density did not affect selection.

TABLE 4. Learning where to search: selection ($\pm$ 95% confidence interval) for place A at various prey proportions. Skunks increasingly chose A as A increased in relative density. S_A is analogous to the probability of choosing place A if both A and B are presented simultaneously. 'Differences Among Individuals' are results of chi-square tests among individual skunks.

Prey Proportions A:B	Selection for Microhabitat A (S _A)	Number of Microhabitats Chosen		Differences Among Individuals (X ² D.F.=2)
		A	B	
0:1	0.32 (±0.02)*	1682	634	0.41
0.2:1	0.36 (±0.03)*	1036	347	0.60
0.4:1	0.38 (±0.03)*	991	295	1.4
1:1	0.41 (±0.03)*	976	179	0.17
1:0	0.50 (±0.04)	976	179	0.77
Half of usual microhabitat density				
0:1	0.33 (±0.02)*	807	305	0.59

* S_A is sig different from 0.5 at $p < 0.05$.

5.4 SEARCH IMAGE

When predators react to prey, they first detect it and then decide whether or not to pursue it. In this set of experiments I studied how the distance at which skunks reacted to the smell of food changed with experience (skunks usually find prey by odor; Rosatte 1985). There are two possible mechanisms for changes in reaction distance to the smell of food: the skunks' ability to detect different odor levels may change, or they may choose to investigate different odor levels (i.e. they alter their prey preference). However, the results of the prey preference experiments showed that skunks do not change preference as a result of past experience. Hence, if skunks change the distance at which they react to the smell of food, then they must actually detect prey at different odor levels. This is the olfactory analogue of a visual search image - the olfactory search image (OSI). The following experiments test whether, in fact, skunks do form olfactory search images.

5.4.1 General Methods

I tested individual skunks on leashes in an outdoor area of short grass. For a leash I used a thin string - to ensure that the skunk would feel nothing pulling at it while it foraged. First, I placed a piece of food on the ground upwind of the skunk. I did this by waiting until I was out of the field of view of the skunk (skunks have very poor eyesight - they cannot see well past about 1 m), then walking away and tossing the food item onto the ground.

Then, as the skunk wandered about, I gradually guided it closer and closer to the food until the skunk raised its head and approached the food. By 'guided' I do not mean in the common sense of guiding a dog on a leash. The only way to influence the direction that a skunk went was to hold the leash steady when the animal moved. The skunk would then stop, turn, and go in another direction; if I actually pulled the leash the animal would attempt to run away. I let the skunk

wander around for several minutes. If it did not react to the smell of the food, then I stopped the animal, it would turn, and if I did this a few times the animal would end up a little closer to the food. Then I would again wait for several minutes to see if there was a response.

The response to the odor of food was very striking. Normally, when skunks are foraging, they move their heads back and forth while sniffing at the ground and wandering about. When they smell food in the air, they raise their heads and walk directly towards the source of the smell. It is very obvious at what point the skunks react to the smell of food. Thus, the operational definition of reaction distance that I used was: the distance from the food item to the location of the skunk when it raised its head. Note that this definition makes no assumptions about whether the reaction point is the point at which skunks actually smell food, or just the point at which they decide to investigate the food.

I noted the distance at which the skunk reacted to the food, wind direction relative to food (although I started upwind of the skunk, sometimes the wind shifted) and time. I repeated this procedure with a series of food items to see how the skunk's reaction distance changed with experience.

5.4.2 Experiment 1

5.4.2.1 Methods

Experiment 1 tested whether skunks increased reaction distance when presented with a sequence of one type of food. I placed dry kibble dogfood pieces on the ground at time intervals of 2-10 min. As soon as a skunk found one food item, I presented the next one. I assumed that the skunks found the dogfood by smell because they wandered about with heads down, then raised their heads in the air and walked upwind directly towards the dogfood. Each trial consisted of 10-16 food

items and I did 6-7 trials per skunk, each on a different day (these also included the first parts of the trials used in the next two experiments).

5.4.2.2 Analysis and Results

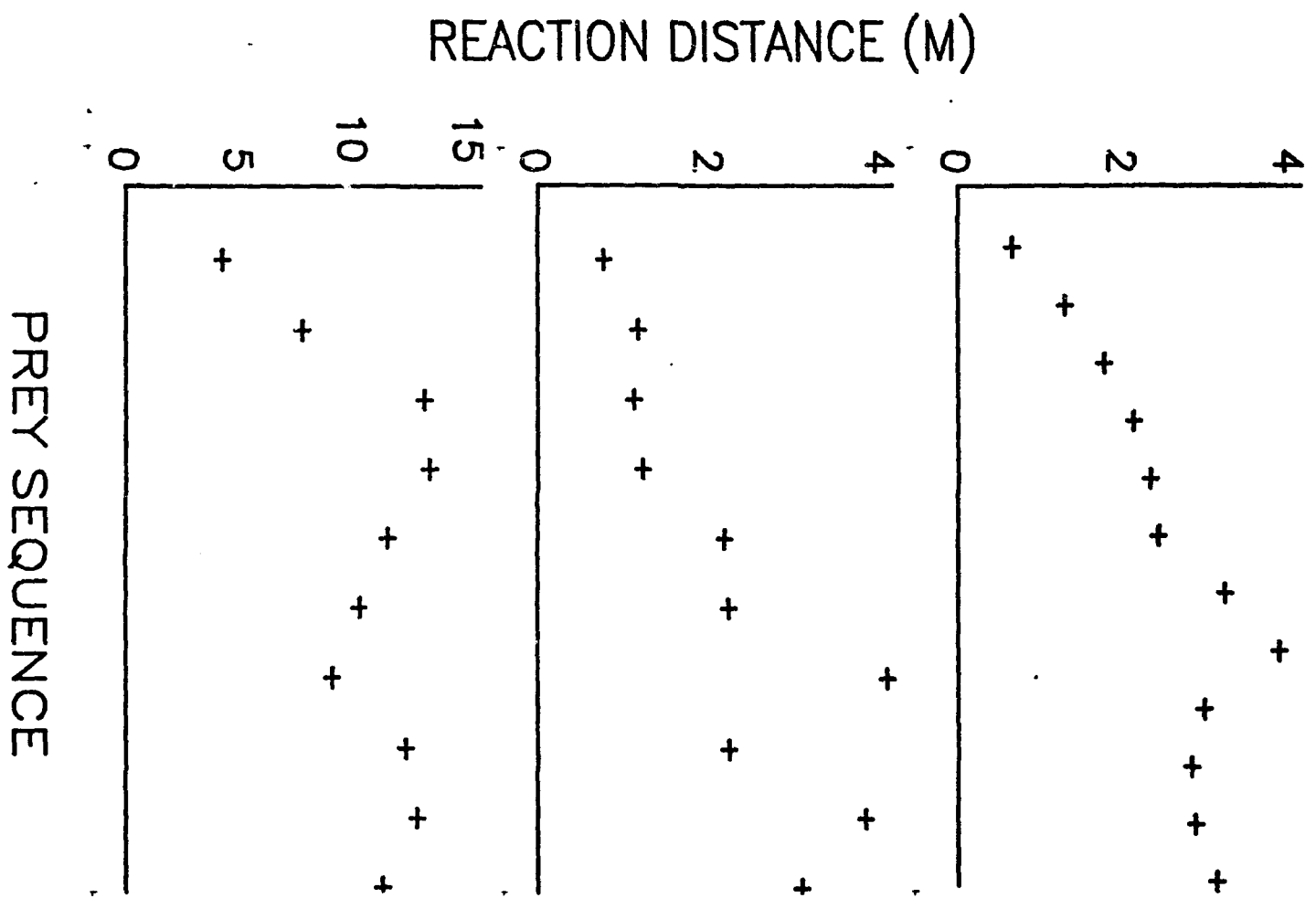
To see if reaction distance changed systematically, I estimated the slope between food sequence number and reaction distance. Slopes were significantly different among trials for 2 of the 3 animals; however, there were no differences among animals (F among animals = 1.84, d.f. = 2,16, $p > 0.05$). Therefore I combined data from all animals and used the among-trial variation to estimate variance of the combined slope.

During trials, skunks reacted to food from farther and farther away (Fig 5; overall mean slope between reaction distance and prey sequence number = 21.7 ± 4.5 , d.f. = 16). This increase was not simply the result of becoming familiar with a novel food item since the experimental animals were fed kibble most of their lives. Also, the increase was not a result of learning a novel situation since the reaction distance increased during every trial, not just the first one. So, skunks shift attention to prey during a feeding session.

5.4.3 Experiment 2

The following two experiments tested for what cues skunks use to shift attention to prey. This experiment tested whether skunks simply shift attention to prey in general, or whether they shift attention specifically to finding prey with a certain sense. If skunks do simply shift attention to prey in general, then the increase in reaction distance shown in the previous experiment should not be affected by skunks finding other foods by other senses, because they are still finding food. However, if skunks specifically shift attention to different sensory stimuli, then

Figure 5. The distance at which skunks reacted to the smell of dogfood increased with prey sequence. Three sample plots.



reaction distance to the odor of food should be affected by finding food by other senses.

5.4.3.1 Methods

The experiment was divided into three periods: in the first period, skunks found 10 - 15 pieces of dogfood as in experiment 1; in the second period, skunks found 30 grasshoppers (*Tettigonioidea*); in the third period, skunks again found 10 - 15 pieces of dogfood.

A skunk feeds on live grasshoppers by hearing them jump, pouncing where they land, then looking beneath its paws (Nams pers. obs.). I tossed dead grasshoppers to the skunks and they found them the same way: by hearing them fall and pouncing on them. I knew that they used sound to detect them because they would pounce even when the grasshoppers landed behind them, presumably out of their field of view.

So, in this experiment, the skunks were presented with food that they located by smell (dogfood), and food that they located by sound (grasshoppers), in the sequence of smell, then sound, then smell again. If skunks do shift attention to the odor of prey, then their reaction distance to dogfood should decrease from period 1 to period 3, due to their finding another type of food by a different sensory stimulus, sound.

5.4.3.2 Analysis and Results

For each trial I estimated (Appendix 3) how much the reaction distance changed from the last piece of kibble eaten in period 1 to the first piece of kibble eaten in period 3. The variance of the difference was given by the sum of the variances of the estimated reaction distances*.

*This requires that the two variables are independent. However, if they are

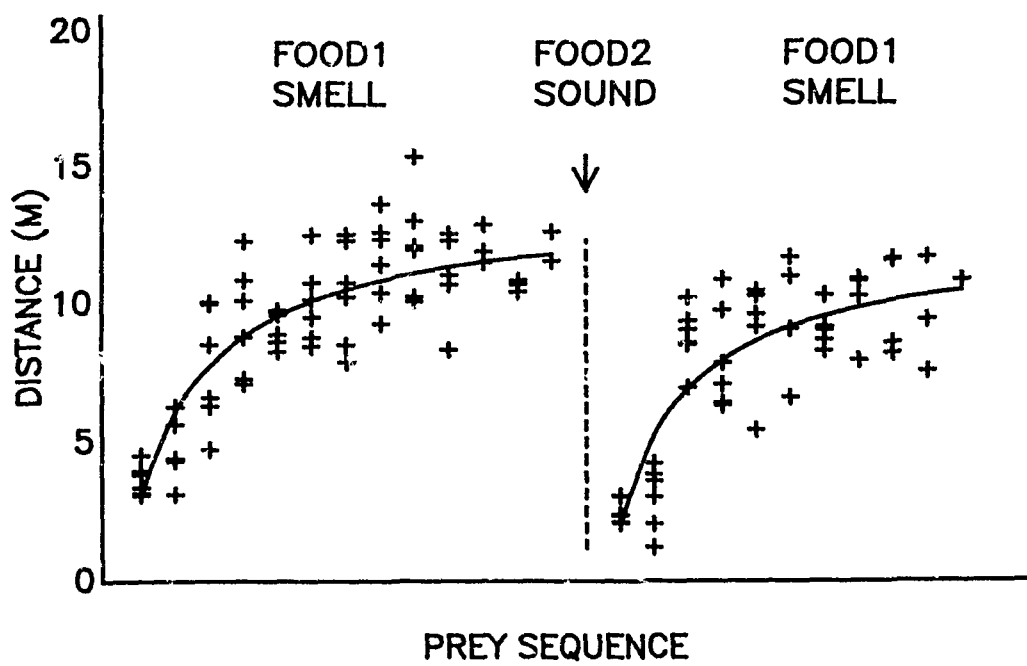
Trials did not differ in the change in reaction distance for each animal. When data were summed over all trials, animals did not differ in the change in reaction distance (F among individuals = 3.05, d.f. = 2,95, $p > 0.05$). Thus I summed the changes in reaction distance over all animals and trials, and included both among- and within-trials components in the variance estimate.

Reaction distance to kibble dropped from a mean of 9.2 m at the end of period 1 to 1.9 m at the start of period 3 (Fig 6). This decrease is both large and statistically significant (mean difference = $7.28 \text{ m} \pm 2.12$, d.f. = 5). Thus, skunks reacted to the smell of kibble less strongly after they found grasshoppers by sound. This drop in reaction distance was not simply due to the amount of time it took skunks to eat grasshoppers since they ate all the grasshoppers in only 7 - 10 minutes (occasionally the interval between two dogfood pieces was this long, without a corresponding drop in reaction distance).

Thus the increase in reaction distance with prey sequence noted in experiment 1 was not just an increase in reaction distance to prey in general, but specifically to prey found by smell. So, when cueing in to prey, skunks switch between the use of sound versus smell.

not, then the error would decrease the variance estimate only if the variables were negatively correlated. This is highly unlikely because if by chance the last reaction distance in period 1 is very high, one would expect that the first reaction distance in the period 3 to be high, not low.

Figure 6. The distance at which skunks reacted to the smell of food1 (dogfood) decreased after they found another food (grasshoppers) by sound. First, parameters A,B,C (from equation 1) were estimated for each trial. For the purpose of plotting only, parameters were averaged over all trials and reaction distances in each trial were scaled to the mean parameter values.



5.4.4 Experiment 3

The following experiment tested whether when skunks shift attention to the odor of prey, they simply cue in to odor in general, or to the specific type of odor. In other words, do skunks cue in to odor in general, or to the specific type of prey?

5.4.4.1 Methods

The experiment was divided into 3 periods, like experiment 2, except that now in period 2 the skunks were fed a type of food that they also found by smell (raw meat). If skunks do cue in to specific types of prey by their smell, then reaction distance to the smell of kibble should decrease from period 1 to period 3 due to their also finding meat by smell.

In period 2 I measured reaction distances as skunks found 7 - 11 pieces of meat one after the other. As soon as a skunk found and ate one piece, I placed the next (2 - 10 min apart). Because the odor of raw meat carries much further in the air than does the odor of dry dogfood, the reaction distances in some of the trials were so far that it was not feasible to measure them (the distances were much farther than the size of experimental area).

5.4.4.2 Analysis and Results

The data were analyzed in the same way as for experiment 2. For each animal, trials did not differ in the change in reaction distance. When data were summed over all trials, animals did not differ in the change in reaction distance (F among individuals = 0.72, d.f. = 2,95, $p > 0.05$). Thus I summed the changes in reaction distance over all animals and trials, and included both among- and within-trials components in the variance estimate.

Over all trials and animals, reaction distance to kibble dropped from a mean of 3.80 m at the end of period 1 to 1.05 m at the start of period 3. This decrease due

to finding another food by smell is smaller than that due to finding another food by sound (experiment 2), but is still significantly greater than 0 (mean difference = 2.55 ± 0.74 , d.f. = 5; Fig 7).

This decrease in reaction distance was not due to the skunks either smelling my scent from the direction of the food or observing me place the food. If it would have been, then reaction distance would not have dropped at the end of period 1, but would have continued to increase. My odour would have been present in all three periods, yet the skunks reacted differently from one period to another.

So not only do skunks cue in to prey by the use of sound vs smell, but they also cue in to finding different types of prey when both are detected by smell.

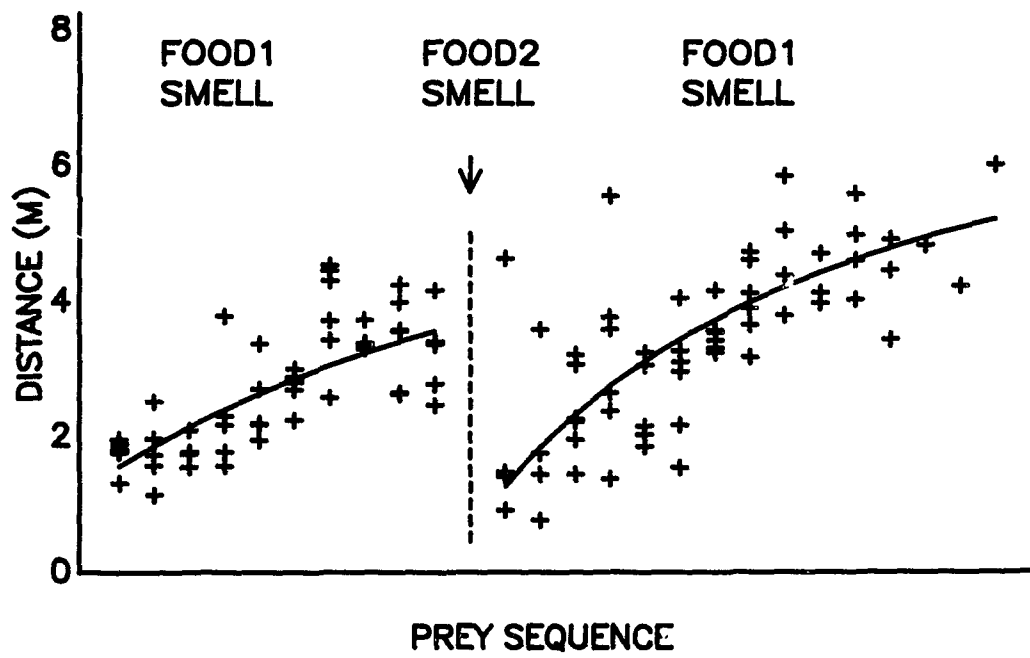
These three experiments clearly showed that the distance at which skunks reacted to specific prey types detected by smell increased with experience. However, this reaction distance dropped after skunks found another prey type by sound or smell. Since skunks do not change prey preference, they must form olfactory search images.

5.5 LONG-TERM SEARCH IMAGE

The previous experiments showed that skunks can form OSI's over one feeding session - that is, over one to several hours. However, in the wild, skunks encounter specific types of prey over longer periods of time than just one day. Various species of insects may be present for several months, and ducks and grouse nest for six to eight weeks (Bump et al. 1947, Keith 1961). Perhaps skunks' OSI's change over long time intervals.

I did two experiments to study long-term search images. The first one measured how the formation of a search image changes from day to day, using small food items that the skunks encountered many times each day. The second one tested

Figure 7. The distance at which skunks reacted to the smell of food1 (dogfood) decreased after they found another food (meat) by smell. Methods as in Figure 5.



whether a search image can be formed over several days, using large food items that the skunks encountered once a day.

5.5.1 Experiment 1

5.5.1.1 Methods

To measure how the formation of a search image changes from day to day I reanalyzed the data from the initial search image experiments. In those experiments I measured detection distance to kibble dogfood during a series of 6 or 7 trials held once a day. Although I did only one trial per day, the days were not always consecutive, because some days the wind was too strong or there were interruptions (e.g. farm machinery driving by), or there was not enough time to test all three animals in a day. In this second analysis, I examined changes in the OSI from trial to trial.

5.5.1.2 Analysis and Results

To mathematically describe the formation of a search image, I estimated the initial and maximum detection distances, and the initial rate of increase in detection distance (Appendix 3) in each trial. Then for each animal I ran linear regressions of the various parameters (Table 5) versus trial number (a measure of time and experience). Since the parameter estimates had very different variances, I used a weighted regression (weighted by variance⁻¹; Searle 1971, Cochran 1977).

The distance at which the skunks initially detected food (C) increased from day to day for skunks 1 & 2, but not for #3 (Fig 8, Table 6); the slopes of the regression lines differed significantly among individual animals (Table 6). Perhaps the results for skunk #3 were due to a poor fit of the asymptotic equation; for example, the C-value on day 7 for skunk #3 is negative 0.13 m, yet it actually detected the first prey item 1.3 m away (Fig 9). When a search image is formed very

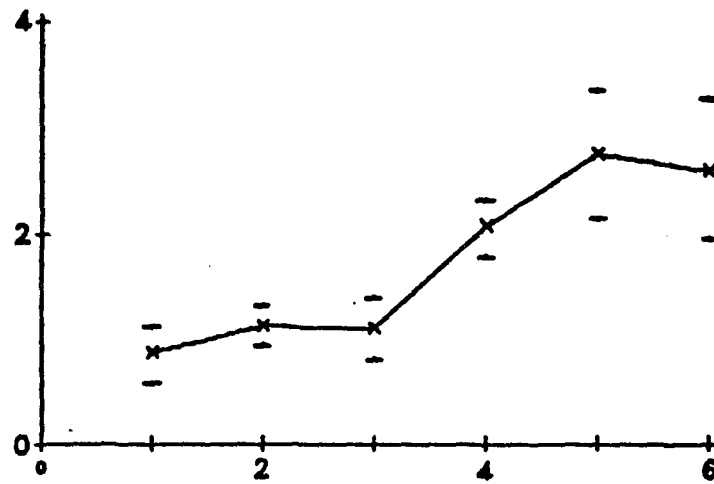
TABLE 5. Long-term search images: parameters. Parameters were estimated by fitting the asymptotic equation (Appendix 3) to the data from each daily search image trial, for each animal. Data are parameter estimate and $\pm \sqrt{\text{variance}}$ of the estimate. 'Estimated Initial Distance' is the initial distance estimated by fitting the asymptotic equation to all the data, while 'Actual Initial Distance' is the distance at which skunks detected the first food item. Distance units are in cm. See Fig 8 for plots of the data.

Trial Number	D.F.	Estimated Initial Distance (C)	Maximum Distance (A+C)	Arctan of Initial Slope (Arctan(E))	Actual Initial Distance
<u>Skunk #1</u>					
1	11	92 ± 92.9	* *	0.139 ± 0.071	50
2	8	67.4 ± 33.0	310 ± 103	0.449 ± 0.325	68
3	8	146 ± 82.8	369 ± 141	0.858 ± 0.864	170
4	8	270 ± 86.9	831 ± 1050	0.299 ± 0.413	310
5	7	359 ± 196	1430 ± 384	1.351 ± 0.197	435
6	7	383 ± 178	1200 ± 275	1.519 ± 0.064	390
<u>Skunk #2</u>					
1	9	49.9 ± 37.6	406 ± 77.6	0.785 ± 0.276	58
2	13	206 ± 64.8	* *	0.194 ± 0.043	235
3	6	97.7 ± 64.3	1410 ± 3510	0.484 ± 0.373	123
4	6	197 ± 28.7	643 ± 317	0.380 ± 0.228	230
5	13	213 ± 180	1390 ± 274	1.303 ± 0.154	300
6	7	312 ± 225	1650 ± 415	1.416 ± 0.125	340
<u>Skunk #3</u>					
1	13	33.9 ± 46.8	* *	0.132 ± 0.101	11
2	5	96.5 ± 61.3	254 ± 92.0	1.688 ± 0.247	97
3	7	140 ± 55.7	387 ± 118	0.730 ± 0.588	150
4	7	49.4 ± 63.1	624 ± 487	0.504 ± 0.390	70
5	11	84.3 ± 33.2	2290 ± 9610	0.197 ± 0.111	60
6	10	150 ± 115	683 ± 171	1.495 ± 0.088	150
7	13	-13.2 ± 115	1860 ± 482	1.073 ± 0.176	130

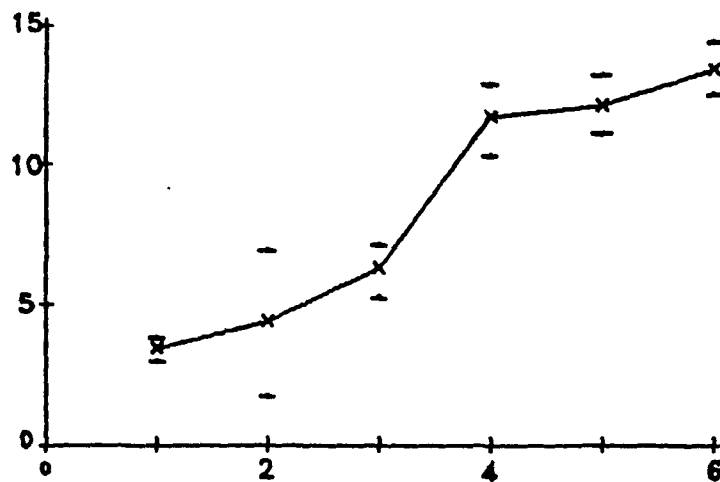
* Estimate for A+C was infinity, but confidence interval included zero, so I considered estimate to be unknown.

Figure 8. Search images changed when skunks found same food from day to day. Plots show how parameters of asymptotic equations that were fitted to detection distance data (Fig 9), changed through time. a) C = initial detection distance; b) $A + C$ = maximum detection distance; c) E = initial rate of increase in detection distance. Bars represent 95% confidence intervals.

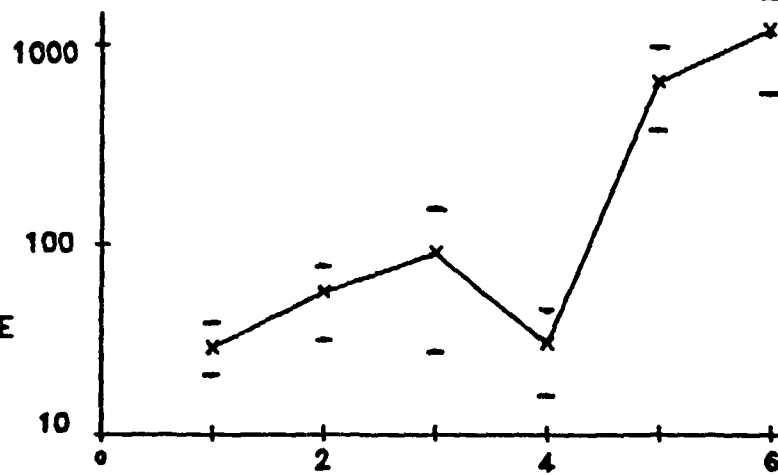
A.)
INITIAL
DISTANCE
(METRES)



B.)
ASYMPTOTIC
DISTANCE
(METRES)



C.)
INITIAL
RATE OF
INCREASE
IN DISTANCE



D A Y

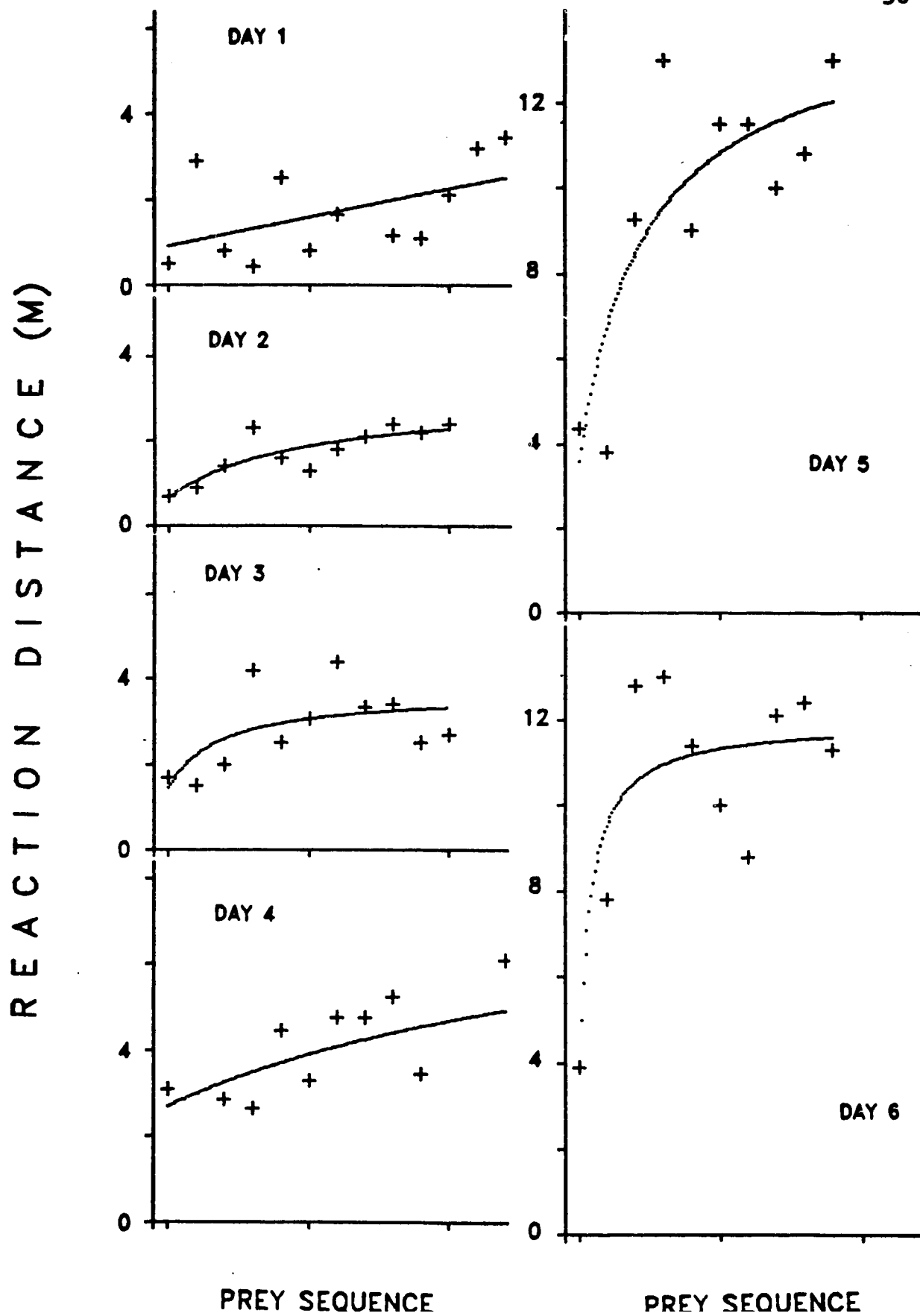
TABLE 6. Long-term search image: changes in search image parameters over several feeding sessions. All parameters increased, except for the two initial detection distances for skunk #3. C is the initial detection distance estimated from fitted asymptotic equation, whereas 'Actual Initial' is the actual detection distance of the first item skunks found. Olfactory search image parameter increases with time when slopes (+ 95% confidence intervals) between sequence of feeding sessions and parameters are significantly larger than zero. Slopes are also shown for individual animals whenever animals differ. 'Differences Among Individuals' is results of F-test among slopes of individual skunks. See Fig 8 for plots of parameters and Fig 8 for plots of actual detection distances.

Detection Distance Parameter	Individual Animal			Differences Among Individuals	
		Slope	D.F.	F	D.F.
Estimated Initial (C)	1	77.7 (± 51) *	53	4.52#	2,180
	2	44.0 (± 29) *	58		
	3	3.1 (± 25)	69		
Actual Initial	1	84.0 (± 37) *	5	10.0#	2,13
	2	48.9 (± 29) *	5		
	3	13.3 (± 25)	6		
Maximum (A+C)	All	191 (± 47) *	148	0.62	2,146
Initial Rate of Increase (E)	1	0.28 (± 0.04) *	49	6.65#	2,169
	2	0.30 (± 0.07) *	54		
	3	0.18 (± 0.05) *	66		

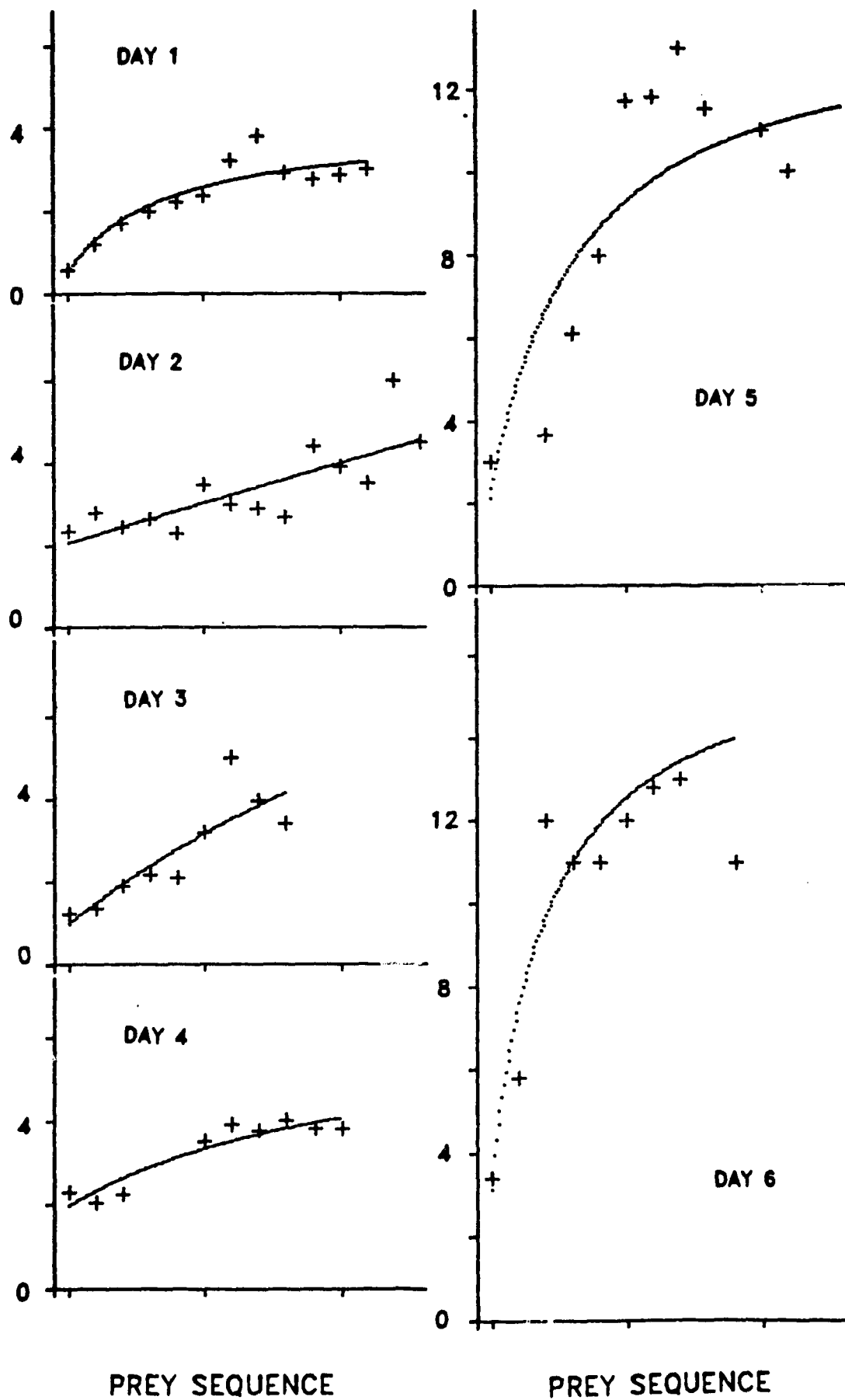
* Slope significantly different from 0 at $p < 0.05$

Significantly different at $p < 0.05$

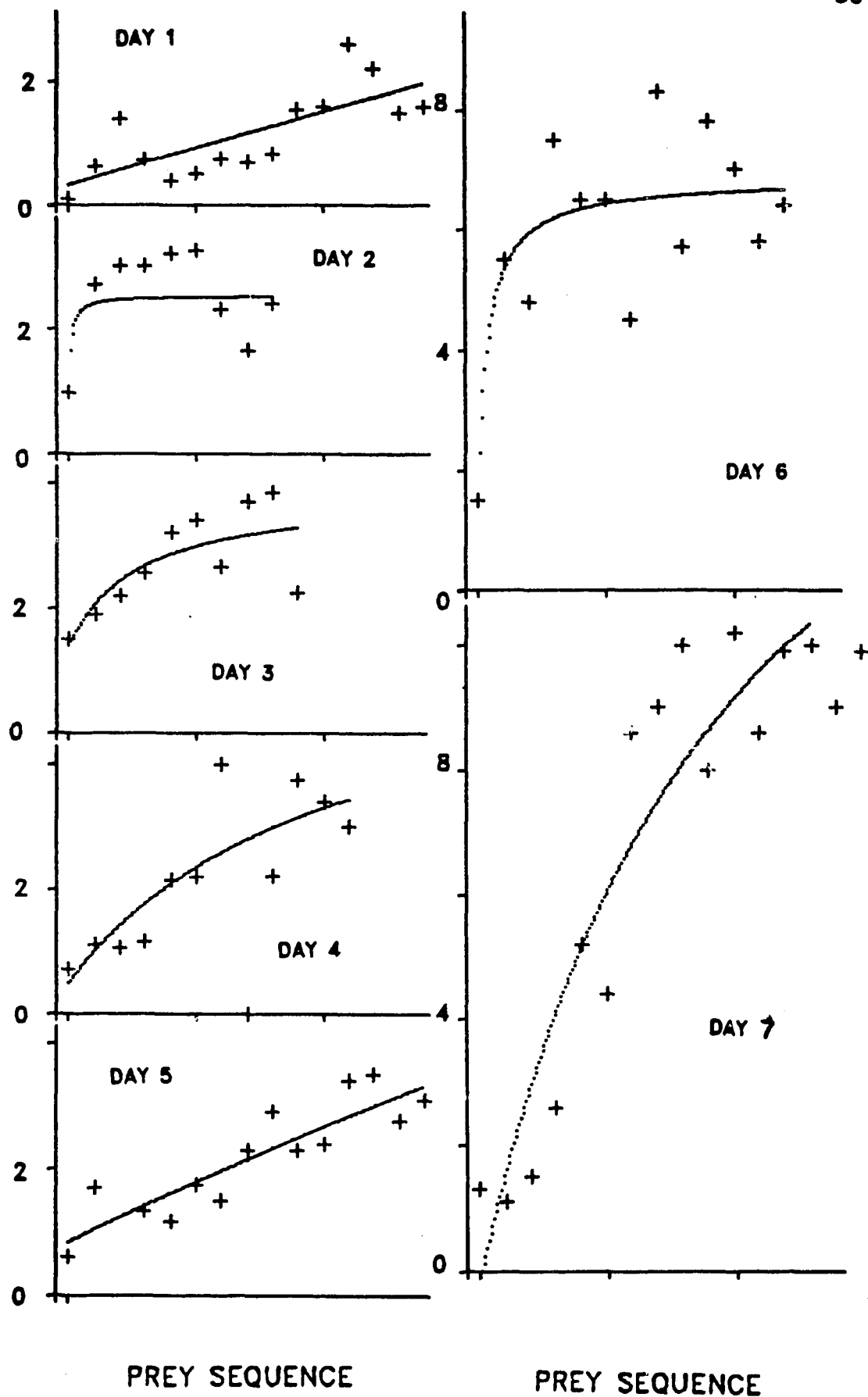
Figure 9. Search images changed when skunks found same food from day to day.
Detection distance versus prey sequence number for successive days for each skunk.
Solid lines represent fitted asymptotic equation. a) - c) represent skunks # 1 - 3.



REACTION DISTANCE (M)



REACTION DISTANCE (M)



quickly (e.g. the last two days) the asymptotic equation does not fit the data well for all of the animals. Detection distance does level off, but initially the relationship may be sigmoidal, not just asymptotic. After about two prey items, detection distance increases rapidly - almost an off/on response. This results in an underestimation of initial detection distance. That C is a poorer estimate for initial distance in the last two trials can also be seen in the large variance of C for these trials (Table 5).

I repeated the regressions, using the actual rather than the estimated detection distance (C) to the first prey item. On one hand, this increased error variation because I used information from only one data point per trial, but on the other hand this minimized the problem of a biased C estimate. Using the actual initial detection distance, there was still no significant increase in initial distance for skunk #3, although the slope was greater than when using C, and there was still a significant difference among slopes for the different individuals (Table 6). Thus, two of the skunks increased initial detection distance to prey from day to day, and the other did not (rather, it showed no increase greater than a rate of 0.35m per feeding session). Therefore we can conclude that some skunks begin detecting prey at greater distances each successive day that they forage on the same type of food, but not all necessarily do so. (In this case it would have been helpful to have had more individuals available).

Maximum detection distance ($A + C$) increased from day to day for all animals (Fig 8), and the slopes of the regression lines did not differ significantly among individual animals (Table 6). From one feeding session to the next, skunks increase the maximum distance at which they can detect prey.

The initial rate of increase in detection distance (E) increased from one day to the next differently among individuals, but the increase was still significant for

each individual (Table 6; Fig 8). Hence, from one feeding session to the next, the rate of OSI formation increases.

In summary, at the start of the first day, the skunks, on average, detected dogfood pellets from 0.5 m away, then initially increased this distance by a rate of 0.1 m/prey item to a maximum distance of 3.4 m at the end of the day. At the start of the last day, they first detected prey from 1.4 m, then initially increased this distance by a rate of 2.0 m/prey item to a maximum distance of 14.3 m at the end of the day. We can see that when skunks feed on many small food items, they form search images faster and to a greater degree from one day to the next.

5.5.2 Experiment 2

All the search image experiments described so far were done with small food items. However, in the wild, not all prey items exist in such small quantities. In the spring, skunks feed on eggs of ground-nesting birds (often ducks or grouse) whose nests can contain up to 14 eggs (Bump et al. 1947, Keith 1961). One such nest is usually enough to satiate a skunk (Nams pers. obs.), and so skunks generally feed on only one nest per feeding session. After finding a nest, skunks often return to the same area the next night (Nams pers. obs.), presumably to search for more. If skunks can form an OSI for nests, it must be the result of very few encounters per feeding session.

In this experiment I tested whether skunks form an OSI when they encounter only one large food item per feeding session. I simulated skunks finding nests of ground-nesting birds on successive nights in the same area.

5.5.2.1 Methods

Instead of real bird nests I used dummy nests as food items. These consisted of four chicken eggs placed on the ground in grass tall enough that they could not be

seen from 30cm away at the eye level of a skunk. To increase the odor of the dummy nests I poked a 1-2mm hole in each egg. Real nests would have a much stronger smell than four whole chicken eggs because of feathers, droppings and the bird at the nest.

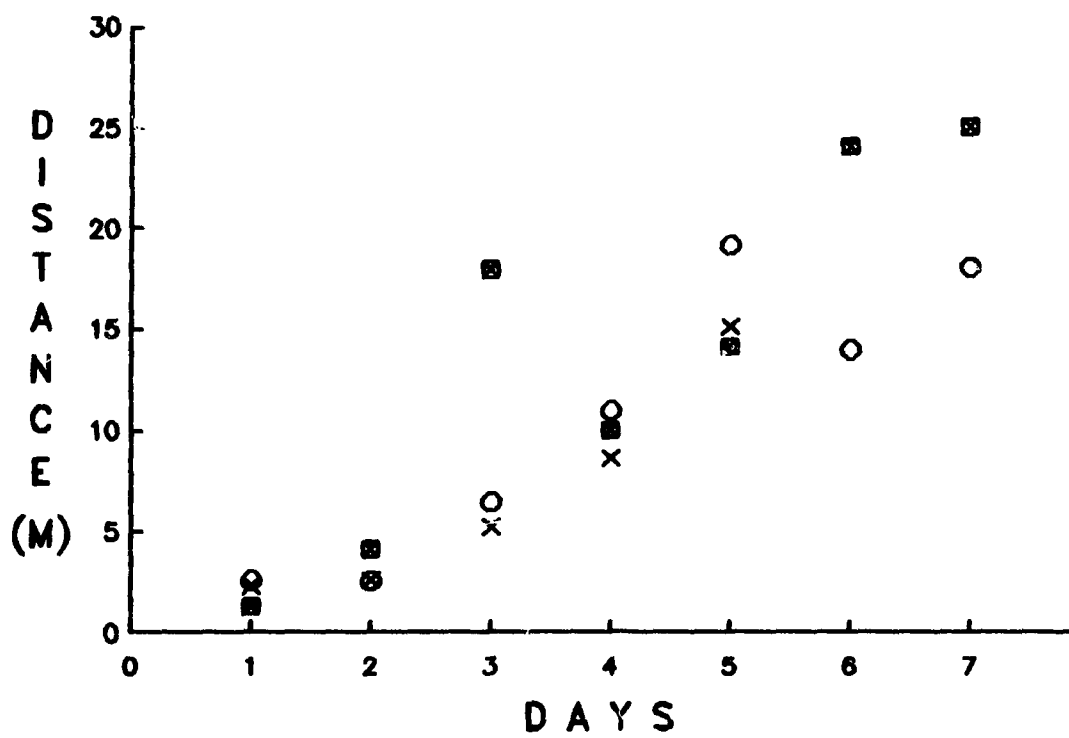
I took each skunk to a grassy area and as in the previous experiments, measured the distance at which it detected a dummy nest. Because of the long detection distances, wind was especially important, so I always placed the eggs upwind and did the experiments when wind speed was very low. I let the skunk eat the eggs and gave it more until it was satiated (6 - 7 eggs in total). This simulated the skunk finding a clutch of duck or grouse eggs (equivalent of 5 - 12 chicken eggs, by volume), which they usually eat until satiated. After the skunk finished feeding, I covered the nest site with a pile of dirt to remove any residual egg smells. This whole procedure was repeated for 7 consecutive days in the same area.

5.5.2.2 Analysis and Results

The distance at which each skunk detected nests increased from day to day (Fig 10), and there were no significant differences among animals in slope of the increase (F among slopes of individuals = 0.41, d.f. = 2,13, $p > 0.05$). Thus, even one encounter of a large food item (such as a clutch of eggs) per foraging session is enough to cause skunks to form an OSI. In just 7 daily feeding sessions, skunks increased their ability to detect dummy nests ten-fold, from an initial distance of about 2.5m to 25m.

From watching the skunks it was obvious that they used the wind; sometimes when following an odour to a nest, if the breeze shifted they would lose the scent. Although they followed scents in the air, they did not follow the scent of my body when I placed the eggs. My scent was not just restricted to the spot where I placed the eggs, because I walked about everywhere. The skunks also did not follow

Figure 10. Detection distance increased from day to day when skunks found only one dummy nest a day. Data shown for each of the three skunks.



physical evidence of my placing the nests (e.g. broken grass) - I followed a circuitous route when placing the nests and the skunks went directly to the nests along the path of the wind.

The latter distance may be close to the maximum distance at which skunks can detect food in the wild (even though detection of dummy nests did not level off; Fig 10). At such long distances, slight shifts in wind direction usually caused my skunks to lose the dummy nest scent, and they had to start searching again. Thus the limitation is physical, not biological. Even though the animals might be able to detect much lower levels of odor, the wind causes them to lose the scent.

5.6 INTERACTION OF SEARCH IMAGE AND HABITAT

Perhaps search images are related to habitat type. Skunks form OSI's, and they also use some habitats more than others (Rosatte 1985). Prey differ both in their odor and in the general habitats they use. When skunks enter a certain habitat, they may already have a search image for the type of prey usually found there. Conversely, when they leave a habitat, they may lose the search image of the prey on which they were feeding.

I tested whether an OSI formed in a certain habitat is affected by skunks entering another habitat where they had previously found a different type of food by sound.

5.6.1 Methods

The experiment consisted of 2 acclimation periods and then a test period. In each acclimation period I allowed skunks to learn to associate food type with habitat type by letting them find food1 in habitat1 by smell, then food2 in habitat2 by sound. In the test, I first measured the distance at which skunks detected a series of pieces of food1 in habitat1. Then I immediately guided them into habitat2, continued

providing food1, and measured the distance at which they detected it. This tested the idea that the skunks would 'expect' to find food2 by sound in habitat2.

The two food types used were meat (food1) and a cooked flour pastry (food2). I placed the meat on the ground and the skunks found it by smell. I tossed the flour pastry to the side or behind the skunks and they turned and pounced on the source of the sound. I chose two adjacent habitats that had a long common border so that I could do a lengthy series of food offerings in one habitat, then immediately move over to the other one. The two habitats were a well-grazed pasture (habitat1) and a young crop field (flax, about 15cm tall; habitat2). I did a total of 8 trials, with 1 to 4 trials per animal. During each trial I consecutively presented 6-10 pieces of food in each habitat.

5.6.2 Analysis and Results

If search image is affected by habitat type, then detection distance to food1 should drop when skunks go from habitat1 to habitat2. If search image is dependent only on the last food type eaten, then detection distance should not drop when skunks enter habitat2 and find food1 there.

I fitted the asymptotic equation (Appendix 3) to the detection distance data (Table 7). Since it is possible that odor carried farther in one habitat than the other, I scaled the parameters (Table 8) from habitat2 in each trial by multiplying A, C and E by

$$K = \frac{A + C \text{ (habitat1)}}{A + C \text{ (habitat2)}}$$

to force the estimated maximum detection distance (A+C) to be equal in both habitats. Then I estimated how much detection distance changed when skunks left

TABLE 7. Search image x habitat type interaction experiment: initial fitting of asymptotic equation (Appendix 3) to detection distance data. Data were fitted for three parts of the experiment: the first acclimation part in habitat1 (Accl), the test section in habitat1 just before going into habitat2 (Hab1), and the test section in habitat2 (Hab2). Data are parameter estimate, $\pm \sqrt{\text{variance}}$ of the estimate. To normalize the initial slope parameter, E, it was transformed by arctan when fitting the equation. Distance units are in m. See Fig 9 for plots of the data.

Trial #	Trial Part	D.F.	Estimated Initial Distance (C)		Maximum Distance (A+C)		Arctan of Initial Slope Arctan(EP)	
<u>Skunk #1</u>								
1	Accl	5	3.50	± 0.977	7.58	± 1.52	1.53	± 0.10
	Hab1	7	4.82	± 0.693	11.13	± 26.0	0.24	± 0.42
	Hab2	8	2.72	± 0.52	7.60	± 1.82	0.69	± 0.34
2	Accl	6	7.46	± 1.64	*	*	1.20	± 0.06
	Hab1	4	11.8	± 1.93	21.62	± 4.19	1.42	± 0.16
	Hab2	5	9.27	± 5.26	21.57	± 11.5	1.41	± 0.33
3	Accl	4	2.60	± 1.94	19.00	± 6.28	1.41	± 0.12
	Hab1	4	7.52	± 1.49	13.08	± 2.23	1.63	± 0.05
	Hab2	4	3.84	± 3.16	113.8	± 72.6	1.47	± 0.08
4	Accl	6	9.28	± 1.54	*	*	0.89	± 0.17
	Hab1	6	10.2	± 1.93	*	*	1.13	± 0.10
	Hab2	4	7.82	± 0.862	16.63	± 6.52	1.46	± 0.16

Skunk #2

1	Accl	4	4.21	± 2.05	16.01	± 3.01	1.58	± 0.02
	Hab1	4	4.97	± 1.66	9.25	± 2.77	1.49	± 0.22
	Hab2	4	3.84	± 1.57	8.65	± 3.64	1.23	± 0.64

Skunk #3

1	Accl	4	1.96	± 1.82	7.92	± 3.05	1.51	± 0.13
	Hab1	4	8.80	± 0.939	10.12	± 1.38	1.60	± 0.84
	Hab2	5	0.933	± 0.741	9.55	± 6.50	0.89	± 0.24
2	Accl	3	19.0	± 1.92	16.10	± 2.85	1.40	± 0.34
	Hab1	3	10.6	± 1.68	74.1	$\pm *497$	0.97	± 0.52
	Hab2	5	3.87	± 1.09	17.87	± 37.5	0.70	± 0.59
3	Accl	4	3.01	± 1.27	13.01	± 2.11	1.54	± 0.03
	Hab1	4	10.0	± 1.70	13.06	± 2.50	1.71	± 0.24
	Hab2	4	7.90	± 1.88	13.10	± 3.61	1.37	± 0.37

* Estimate for A+C was infinity, but confidence interval included zero, so I considered estimate to be unknown.

TABLE 8. Search image x habitat type interaction experiment: standardization of detection distance data in the two habitats. K is the calibration constant to adjust detection distances in two habitats to same maximum distance. 'Estimated Detection ...' was calibrated by K. Values for detection distance are estimate, $\pm\sqrt{\text{variance}}$.

Individual Animal	Trial #	K	Last Prey Sequence # in Habitat 1 (I)	Estimated Detection Distance at Last Prey Sequence in Habitat 1 Dist(I)	
Skunk #1	1	0.827	10	6.70	± 0.600
	2	0.927	7	19.6	± 1.28
	3	2.12	7	13.4	± 0.731
	4	undefined	7	23.1	± 1.93
Skunk #2	1	1.19	7	9.02	± 0.948
Skunk #3	1	0.436 99	7	10.1	± 0.383
	2	0.727	6	18.3	± 1.61
	3	1.00	7	13.1	± 0.692

habitat1 and entered habitat2, and the differences in initial distance (C) and initial slope (E) between habitats 1 and 2 (Table 9).

One problem with this scaling is that it does not include the uncertainty in K (I estimated $\text{var}(KC)$ by $K^2\text{var}(C)$, ignoring the variance of K). This problem was minimized because there were no significant differences among animals for any of these parameters, so I could combine estimates over all trials and calculate the variances of the joint means from among-trial variances only. The individual variances (the $K^2\text{var}(C)$) were then only used as weighting factors, not as estimates of parameter variances.

As soon as skunks entered habitat2, detection distance for food1 dropped (from 10 m in habitat1 to 4 m in habitat 2; Fig 11; Table 10). Not only did detection distance drop, but the initial detection distance of food1 in habitat2 was even lower than the initial detection distance in habitat1 (Table 10). Olfactory search images interact with habitat type.

5.7 FORAGING PATTERNS

During some of the previous experiments, I noticed that skunks changed their behavior while hunting for and eating different types of food. For example, when searching for meat, they tended to keep their heads up in the air more than usual. Such changes may occur for two reasons: the first is that skunks behave differently simply because they are eating different types of food; the second is that skunks may change their foraging behavior to enhance prey detection. For example, when foraging for a food that they can smell from far away, skunks may raise their heads more than usual simply because they smell food in the air, or because they find it easier to detect the smell of food in the air with their heads up. The latter type of behavioral change may cause skunks to find a given food more easily (but other foods less easily), and thus may be another form of switching.

TABLE 9. Search image x habitat type interaction experiment: differences in various search image parameters for each trial between skunks searching for food1 in habitat1 and habitat2. The two rows contain estimates and $\sqrt{\text{variance}}$ of the estimates. 'Acclimation' refers to the first of the two acclimation parts carried out in habitat1.

Last1 = Estimated last distance of test in habitat1
 First2 = Estimated first distance of test in habitat2.
 First1 = Estimated first distance of test in habitat1.
 Angle1 = Initial angle($\arctan(E)$) of test in habitat1.
 Angle2 = Initial angle of test section in habitat2.
 FirstAccl = Estimated first distance in acclimation .
 AngleAccl = Initial angle of acclimation.

	Skunk #1				Skunk #2		Skunk#3		
Trial #	1	2	3	4	1	1	2	3	
Last1	-3.98	-10.3	-9.56	-15.3	-5.18	-9.17	-14.4	-5.20	
-First2	0.80	5.41	3.24	2.11	1.83	0.83	1.94	2.00	
First1	-2.1	-2.53	-3.68	-2.38	-1.13	-7.87	-6.73	-2.1	
-First2	0.87	5.60	3.49	2.11	2.28	1.2	2.00	2.53	
Angle1	0.45	-0.01	-0.16	0.33	-0.26	-0.71	-0.27	-0.34	
-Angle2	0.54	0.37	0.088	0.19		0.87	0.79	0.44	
FirstAccl	-0.78	1.81	1.24	-1.46	-0.37	-1.03	-15.1	4.89	
-First2	1.11	5.51	3.71	1.76	2.58	1.96	2.21	2.27	
AngleAccl	-0.84	0.21	0.06	0.57	-0.35	-0.62	-0.7	-0.17	
-Angle2	0.35	0.34	0.14	0.23	0.64	0.27	0.68	0.37	
D.F.	7	4	4	5	4	4	4	4	

Figure 11. Search image x habitat interaction. Skunks formed new search image for food1 when they went from habitat1 to habitat2; skunks had previously been entrained to food1 in habitat1 and food2 in habitat2. First, parameters C,A,E (from equation 1) were estimated for each trial. Then, to take into account inherent differences in habitats, parameters for habitat2 were scaled so that maximum detection distance was the same in the two habitats. For the purpose of plotting, parameters were averaged over all trials and reaction distances in each trial were scaled to the mean parameter values.

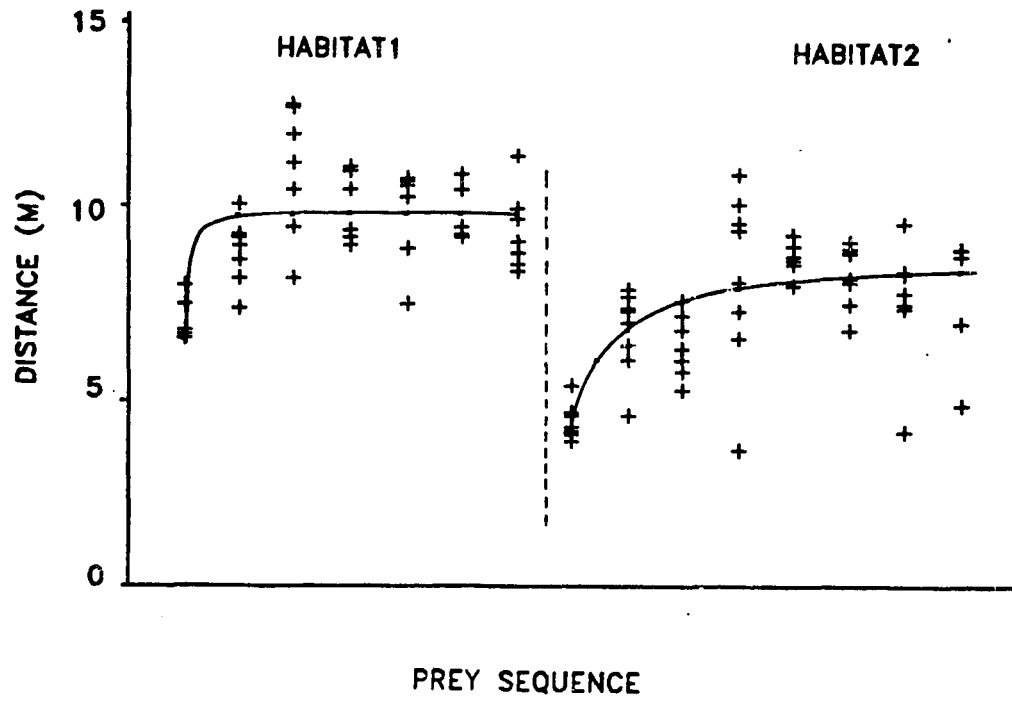


TABLE 10. Search image x habitat interaction. Skunks formed new search image for food1 when they went from habitat1 to habitat2; skunks had previously been entrained to food1 in habitat1 and food2 in habitat2. Differences ($\pm$ 95% confidence interval) in various search image parameters between skunks searching for food1 in habitat1 and habitat2. 'Acclimation' refers to the first of the two acclimation parts carried out in habitat1. All D.F. = 7. See Fig 11 for plot of detection distances in the two habitats.

Change in Detection Distance Parameters

From Habitat1 to Habitat2	Mean	
Detection Distance	-7.36	(± 3.2) *
Initial Detection Distance	-3.86	(± 2.3) *
Initial Detection Distance From Acclimation to Hab2	-0.77	(± 0.18) *
Initial Slope	-1.67	(± 4.32)
Initial Slope From Acclimation to Hab2	-0.030	(± 0.376)

* Significantly different from 0 at $p < 0.05$

The following experiment separates these two effects on skunk behavior. I ask whether skunks change their foraging pattern simply because they detect certain foods, or do they learn a behavior because they detected certain foods, or types of foods, in the past?

5.7.1 Methods

The effects of finding and expecting to find foods were separated as follows. I allowed the skunks to forage outdoors for a certain type of food, then removed the food and described foraging behavior after food was removed. Any differences in behavior between the before-food and after-food intervals are due to skunks expecting to find food.

The experiment had three periods. First, I described foraging behavior of skunks for 30 min in a grassy area without adding food. This gave a baseline description for behavior. Second, I fed the skunks dead grasshoppers for 30 min (they detected them by sound, as in the previous search image experiments), and then described the skunks' behavior for 30 min immediately after they finished eating the grasshoppers. Third, I repeated the whole procedure, but rather than feeding them grasshoppers, I fed them meat, which they detected by smell.

For each replicate, I did all periods of each trial on the same day, to ensure that factors such as wind and other odors in the air would be as similar as possible among the after-meat, after-grasshopper and baseline intervals. This procedure assumed that 30 minutes of searching for and feeding on prey removed the effects on behavior of previous intervals. I did 2-3 trials with each animal, for a total of 8 trials.

I described the skunks' behavior by watching them and talking into a tape recorder. While foraging, skunks typically walk around, sniffing, with their noses to the ground. They sometimes raise their heads and lower them again, turn their

heads to the side, turn their bodies, stop and dig, and stop and eat. I noted each time a skunk stepped, stopped, turned its head or body (and compass directions of these two types of turns), raised its head (skunks usually keep their heads down when they forage), dug or ate. For steps, I noted each time one specific leg stepped.

Later I timed the duration of all of these behaviors by using a microcomputer with an event recorder program. In using this program, I listened to the tape recorder and hit different keys when different events occurred.

I described foraging patterns by various measures such as time per step, and steps between each body turn, head turn, all turns, head up, digging and feeding.

I measured the walking speed of skunks as mean time per step. I divided total time by number of steps, and included the time between any two steps in the total time only if no other behaviors occurred between those steps. This measure estimated walking speed while skunks were walking only, not digging or feeding.

For the rest of the estimates, I wanted to measure average distances that skunks travelled between behaviors. However, I could not measure actual distances because I would have disturbed the animals and because they moved too quickly. Hence I used numbers of steps between behaviors. I did not use time because the skunks varied their speed (the distance between steps also varied, but not as much as time).

I measured investigation in several ways: general investigation by steps between body turns (tortuosity of foraging path), head turns and all turns; investigation of smells in the air by steps between head up; and investigation of smells underground by steps between bouts of digging.

I measured detection of food (that was present throughout all periods of the trial) by steps between each bout of feeding. Since I added no food during any of the periods that I recorded, if skunks did find food, it was present naturally.

5.7.2 Analysis and Results

The variances for these parameters were very different among trials and varied with the mean, so I transformed time between steps by a log transformation (the exponential distribution typically describes time between events) and steps between each behavior by a square root transformation (the Poisson distribution typically describes numbers of events, and the square root transformation normalises Poisson distributed data). Despite the transformations, variances were still different among trials (although not as much as before) so I weighted the parameters by var^{-1} when estimating combined means (Cochran 1977).

For each trial and all parameters, I calculated differences between the various periods of the experiment (variance of the difference between two parts of the experiment is the sum of the individual variances if independent). Then, I found the combined mean difference over all trials. Variance of the combined mean included among-trial variation only, since there were significant differences among trials for most parameters. For all variables and all comparisons (a total of 21), only 2 were significantly different among animals, so I felt confident about combining data for all animals.

The behavior of skunks altered after they found food (meat) by smelling it in the air. They walked faster and straighter and kept their heads up more, but turned their heads, fed and dug less (Table 11). After skunks found food by hearing it (grasshoppers), they kept their heads down more and dug less than usual. Thus, skunks changed their behavior as a result of previously finding food.

6. DISCUSSION

I have shown that skunks can use a number of different mechanisms to switch on to (increase selection for) prey that increase in density. Although skunks do not

TABLE 11. Effect of finding food in the past on foraging behavior. Skunks changed foraging behavior after searching for meat or grasshoppers. 'Baseline' is foraging without any food added. 'Grasshoppers' and 'Meat' are foraging after exposure to grasshoppers, which skunks find by sound, and meat, which they find by smell in the air. Mean values (95% confidence interval) are for various foraging parameters. Data were first transformed, then mean and confidence intervals calculated, then these transformed back. Units for 'Time per Steps' are seconds, and for '# Steps' between each behavior are steps. D.F. = 6 for all.

	Baseline	Grasshoppers	Meat
Time per Step (sec)	7.24 (2.18-24.0)	7.60 (7.00-8.33)	4.89* (4.31-5.58)
# Steps between Body Turns	2.03 (1.54-2.56)	2.17 (1.69-2.72)	4.89* (2.40-3.72)
# Steps between Head Turns	3.44 (2.28-4.80)	2.69 (1.99-3.50)	5.11* (3.57-6.92)
# Steps between All Turns	1.24 (0.92-1.59)	1.14 (0.86-1.46)	2.04* (1.69-2.43)
# Steps between Headups	5.02 (2.66-8.12)	7.62* (4.08-12.3)	2.60* (2.02-3.24)
# Steps between Feedings	24.6 (16.3-34.6)	28.1 (12.3-50.4)	188* (110-286)
# Steps between Diggings	10.4 (7.02-14.5)	27.7* (13.5-46.9)	30.8* (18.7-46.0)

* Significantly different from baseline mean, at $p < 0.05$

change prey preference, they do learn where prey are found (microhabitats), they form olfactory search images (both short and long term, for both many small items and few large ones), they form OSI's in relation to habitat type, and they use different foraging tactics when searching for different types of prey.

Skunks use all these switching mechanisms, yet they are not unique among generalist predators. Many examples in the literature show that generalist predators use one or other of these mechanisms. Indeed, switching is very common among such predators, even though they are generally considered to eat everything nonselectively. Of the various switching mechanisms that I found, only olfactory search images have not been found before (visual search images have been found). Thus, different mechanisms of prey switching by a generalist predator may be a more common practice than previously thought.

6.1 PREY PREFERENCE

The most obvious way for predators to change prey selection is to actually change the type of prey chosen. However, skunks did not switch prey preference in my experiments, even though the tests were a liberal test of change in preference (they erred on the side of showing preference). Since wild skunks encounter prey sequentially rather than simultaneously, and since alternative prey encountered in the wild are likely more different in preference than foods offered in these experiments, wild skunks are presumably even less likely to switch prey preference (Murdoch and Oaten 1975).

However, many other animals do change prey preference. When offered a choice between two food items, rainbow trout tend to select the type they have recently fed upon (Bryan 1973). When Acanthina snails feed upon certain mussels and barnacles, they selectively attack the more abundant prey. When the snails hunt, they move over several prey, contacting them with their tentacles and foot before

they attack one (Murdoch 1969). These animals do not form search images because they change prey preference, not prey detection. Hence, although some predators do switch by changing prey preference, skunks do not.

Although my experiments showed that skunks do not increase preference for those prey on which they have recently fed, the experiments considered learning over only one feeding session. Perhaps skunks change prey preference over longer time intervals. If so, I would expect them to decrease preference rather than increase it. While raising the skunks, I noticed that they 'enthusiastically' ate a new food; however, if they ate nothing else for a long time (weeks), they began to reject it. As well, Curio (1976, p 29) noted that "after having fed on a restricted diet, predators tend to switch to prey hitherto neglected". Such a long-term change in preference would then be in the opposite direction of switching to more common prey, and would not cause density-dependent predation.

6.2 LEARNING WHERE TO FIND FOOD

Prey preference refers to what predators choose once they are near prey. However, predators may also change how they approach prey, that is, they can learn prey microhabitats or where prey are found. Royama (1970) first suggested this idea when he found that great tits feed their nestlings prey items in runs. He concluded that the tits learned where to find particular insects; when they then looked in certain types of places for specific insects, they did not find other insects that used other types of places.

My side choice experiments showed that skunks learn where to find preferred foods, and the place experiments showed that skunks learn what types of places to find food in. Therefore, skunks can switch prey selection by learning where to find prey (small scale).

The place experimental design gave a conservative measure of switching

since I measured selection over the whole trial, but compared it to food density at the start of the trial. During the trial the food eaten was not replaced, and thus food densities changed and approached each other. For example, although food densities may have started off as 0.4:1, during the trial a skunk ate food and changed food densities to near zero (equal) at the end of the trial. During the trials, skunks were exposed to and selected types of places based on some intermediate prey density between 0.4:1 and 0:0 - not the extreme 0.4:1 that I recorded. If skunks were actually exposed to this extreme prey ratio throughout the whole trial, we would expect them to show stronger selection than measured. Therefore, skunks likely switch what types of places they look for food in even more than measured.

Although I kept the amount of food under containers B constant, they were never all empty. I am sure that animals readily learn where food is if it is found only in one type of place. The important and interesting question is whether they can change what types of places to look for food when it is found in more than one type of location.

Other people have also shown that animals learn places. Murdoch et al. (1975) placed guppies (Poecilia reticulatus) in an aquarium with Drosophila on the water surface and tubificid worms on the aquarium bottom. When the relative density of tubificid worms was increased, the guppies changed from spending most of their time near the top of the aquarium to the bottom. The guppies learned where different types of prey were found. Glaucous-winged gulls (Larus glaucescens), foraging in the rocky intertidal zone in the Aleutian Islands of Alaska, usually select for barnacles (Balanus glandula) and mussels (Mytilus edulis), but during spring low tides these species are almost entirely abandoned in favor of sea urchins, chitons and limpets, which are then exposed (Irons et al. 1986). Rainbow trout switch to and from amphipods even in the absence of alternative prey. Once

amphipod abundance on the bottom of an aquarium falls below some threshold value, trout stop searching for them, and spend their time swimming in the water column (Ware 1971, cited in Murdoch and Oaten 1975).

In all of the above studies, the predators shifted from selecting for one prey to selecting for the other. In my experiment, skunks increasingly selected for container A (egg carton tops) with increasing prey density, but they never selected for A (S_A was never greater than 0.5) at any prey density - even when B had no food (a prey density ratio of 1:0; Table 4). This underscores an important point: for a predator to switch on to a prey type, it does not have to select for it at all. It is sufficient for the predator to merely increase selection with increasing prey densities, even if it still selects against that prey. The important thing is that selection, and thus percent predation, increases with increasing prey density. Therefore, if one were studying food habits as a preliminary step to measuring the effect of some predator on prey, one could not discount a prey type just because the predator selected against it.

There are two main reasons why a predator may not select for a place. First, selection for types of places depends on the properties of these places. In my experiments, container A might have been harder to see because it was small and white, compared to B being large and black. These physical differences lead to differences in detection and therefore, different baseline predation rates on prey. Second, selection for a type of place is not determined just by properties of that - it is always relative to others. If B is selected more, then A is selected less. However, switching among prey, and therefore, density-dependent predation, will not be affected by these types of differences just as long as they do not change when prey density changes.

In the wild, the types of places that prey reside in differ not only in the

probability of detection, but also in density. However, skunks did not select differently for A when microhabitat densities were 1/2 of the usual densities (Table 4). Thus, within the range of densities of these trials, density of places did not affect microhabitat selection. Note that in this comparison prey density per place was kept constant, but prey density per area was actually halved. This means that prey density per place is the important factor affecting this selection, not prey density per area.

6.3 SEARCH IMAGE

Predators can also switch by altering their mechanism of prey detection - they can form search images. Although all previous work on search images has dealt with visual ones, these are very similar to the olfactory ones I have described for skunks - both in mechanism and in effect on population dynamics.

Tinbergen (1960) was the first to suggest that predators form search images. He noticed that, when an insect increased in density in the environment, it took some time before it appeared in the diet of great tits (Parus major). However, when it did appear, it was eaten in greater proportion than that found in the environment. Tinbergen suggested that great tits 'learn to see' prey. Dawkins (1971a,b) rigorously tested this idea. She showed that chicks ate different-colored grain in runs, but that chicks did not change preference for the grains. They formed search images for first one color, then another. Pietrewicz and Kamil (1979) trained blue jays (Cyanocitta cristata) to respond differentially to the presence or absence of Catocala moths in projected images. The blue jays could increasingly detect the moths with successive encounters with one cryptic prey type, but not when searching for two species in a series of slides. They could form only one visual search image at a time.

Despite these few good studies, it is hard to prove that visual search images are used since it is difficult to tell exactly when an animal sees an item of food (Lawrence and Allen 1983). However, it is easy to tell exactly when skunks react to

the smell of food (they raise their heads and walk directly toward food). Although Tinbergen's original definition of visual search images mentioned that the prey were camouflaged, that is not necessary for the formation of search images (Lawrence and Allen 1983). That just ensures that differences in predation rate are due to differences in detection, not preference. The problem does not exist with olfactory search images because it is so easy to tell when skunks detect prey.

Skunks exposed to a certain type of food at first did not react to it until they were very close; with increased exposure, they reacted to it from further and further away. Because skunks did not change preference in the preference experiments, I argue that the increased reaction distance observed was not the result of increased preference. Rather, since they did not change preference, the skunks must have formed olfactory search images; that is, they 'learned to smell' prey.

I have used the results from the preference experiments to argue that when skunks increase the distance at which they react to the smell of prey, they do not change preference. In the preference experiments, skunks could choose foods on the basis of both odor and sight, whereas in the reaction distance experiments, skunks could find food only using smell. However, this affects my conclusions only if skunks primarily used sight and neglected odor to choose food in the preference experiments. Since skunks depend mostly on odor to find food in the wild, it is unlikely that they would switch preference based on odor during the reaction distance experiments while not switching preference based on odor and sight in the preference experiments. Therefore skunks must actually detect prey at lower odor levels.

This process is the olfactory analog to a visual search image, and is the first evidence that animals can form short-term olfactory search images. To date, the term 'olfactory search image' has been used in two other ways, but neither is

analogous to a visual search image or to the olfactory search images formed by skunks. Rattlesnakes (Crotalus spp and Sistrurus catenatus) have been said to form OSI's when they eat only prey that they themselves envenomate (Duvall et al. 1978, 1980). However, this is not a change in the ability to detect prey (i.e. formation of a search image), but rather is a way of remembering what prey they envenomated. Yellowfin tuna (Thunnus albacares) have been said to form OSI's when they gradually change their response to new prey odor level over a period of several months (Atema et al. 1980). However, they were not shown to switch back to the odor of the initial prey. In addition, the long time for this change to occur is not analogous to the short term (minutes to hours) change of visual search images. Such a lengthy period suggests that the changes might be physiological, not merely behavioral as in visual search image formation and olfactory search image formation by skunks.

Although search images were previously thought to be exclusive to vision, I have showed that they are also formed with olfaction. Perhaps, then, search images can be formed with all the senses. My experiments showed that search images of different senses interact - skunks lose olfactory search images after hunting by sound. We know that visual search images are non-overlapping (Dawkins 1971a,b, Pietrewicz and Kamil 1979); perhaps, then, search images formed among different senses are also non-overlapping. That is, perhaps the skunks first formed olfactory search images for dogfood, then auditory ones for grasshoppers, then olfactory ones again for dogfood - but not both at the same time. Thus, when predators search for prey, they may form search images with any sense, but use only one search image at a time. Therefore, whatever mechanism is used to form visual search images might be a general one used to form search images with all the senses.

6.4 INTERACTION OF SEARCH IMAGE AND HABITAT

Predators may form search images in different ways in different habitats. The search image and habitat interaction experiment specifically showed that OSI's were lost when skunks entered a different habitat, one in which they had previously found food by sound. There are several ways this could happen: 1) skunks may naturally expect to find different foods when they enter different habitats, independent of past experience, 2) skunks expected to find another food when they entered habitat2, 3) skunks expected to find another food, using the sense of sound rather than smell, when they entered habitat2, and 4) skunks expected to find food2 when they entered habitat2. My experiment showed that OSI's do interact with habitat, but it does not differentiate among these explanations. However, the OSI experiments showed that skunks did not increase reaction distance to prey in general, nor did they simply switch between finding prey by the sense of hearing versus that of smell; rather, they switched between specific prey. Hence I think that of explanations 2 - 4, number 4 is most likely. In order to separate between 1 and 4, however, we need to measure reaction distance of skunks when they enter another habitat in which they do not expect to find any specific prey (i.e. no previous exposure to that habitat).

Such an experiment would answer the question of whether predators 'lose' search images when they leave a habitat. There is one example for the opposite question - do predators 'remember' search images when they enter another habitat? Searching images of carrion crows (Corvus corone corone) for baited red mussel shells (Mytilus) operate more efficiently in those areas where they have been previously reinforced (Croze 1970). Joining the two questions, is the relationship completely a one-habitat one-search image relationship? We do not know yet.

6.5 FORAGING PATTERNS

To increase their chance of finding food, predators may change the way they search for it. In the foraging pattern experiment, I showed that skunks altered their behavior while feeding, not simply because they detected certain foods, but because they had detected them recently. After skunks found food by smelling it in the air, they walked faster and straighter, kept their heads up more, and turned their heads, fed and dug less than usual (Table 11). After skunks found food by hearing it, they tended to keep their heads down more and dig less than usual.

Although I did not measure probability of detecting prey (because I could not remove the effects of search image formation), I can suggest how some of the observed changes in behavior might affect prey detection. First, consider the properties of the foods offered. Odor from meat is carried in the air as opposed to on the ground, and carries further and is less patchy in time and space than sound from grasshoppers. Sound from grasshoppers comes from the ground (where they land), does not carry as far as odor and is patchy in both time and space. During all experimental treatments, there were additional odors in the air, odors and sound from insects in the grass, and odors from underground insects. These are a blend of the general properties for meat and grasshoppers, except that insect odor is localized and on the ground.

Next, consider the skunks' behavior when they searched for food using smell, and compare it to normal baseline foraging, or to searching for food using sound. When skunks searched for food by smell, they kept their heads up more, increasing the chance of their detecting odors in the air. They also turned their heads less; turning their heads often was not necessary because if there was no meat odor in the air in front of them, there would not have been any at their side. Lastly, they walked faster and straighter, increasing the chance of detecting foods that were more

predictable in time and space. Conversely, each of these changes in behavior decreased the chance of hearing grasshoppers.

When skunks searched for food by sound, all of the above-mentioned behaviors changed in the opposite direction, increasing the chances of their hearing grasshoppers. However, skunks' behavior while hunting by sound was not very different from baseline foraging behavior (although they may have tended to keep their heads lower more than usual; $p < 0.08$). Likely this occurred because grasshoppers and prey available during normal baseline foraging were both found on the ground and were both patchily distributed.

The results also show some evidence for actual switching. When skunks searched for food by sound or smell, they dug and fed less than usual. This means that, if we assume that other prey and odors in the ground remained constant throughout all trials, the probability of detecting these other prey dropped as a result of skunks searching for food by sound or smell. We cannot say whether the drop was a result of the change in foraging behavior or a result of the formation of search images for grasshoppers and meat; however, switching did occur.

For a change in behavior to cause switching, it is important that it not only increase the chance of finding one kind of prey, but that it also decrease the chance of finding other kinds of prey. Each type of searching behavior must be specialized for certain prey. For example, when pigmy owls (Glaucidium gnoma) are intent on small mammals, they perch on the tops of trees and scan the ground below; but when they ambush songbirds, they hide in tight bunches of conifers (Scherzinger 1970, cited in de Ruiter 1976). Both American crows (Corvus brachyrhynchos) (Sugden and Beyersbergen 1986) and carrion crows (Tinbergen et al. 1967) first find nests of ground-nesting birds when flying, but then land and search on foot for other nests nearby. This stresses an important point. As with skunks, these owls and crows

did not simply change behavior in response to changes in density of prey, but to the type of prey. Such changes in foraging are thus qualitative (dependent on type of food) not just quantitative (dependent on amount of food).

6.6 OTHER SWITCHING MECHANISMS

Animals may learn a new foraging tactic in a new situation. This is not the same as changing foraging patterns and does not result in switching unless the predator alternates between the tactics from then on, depending on relative prey densities. For example, Alcock (1973) did a foraging experiment with red-winged blackbirds (Agelaius phoeniceus), in which he placed food in holes drilled in wood. Initially, the birds walked around and peered into or probed individual holes; soon they switched to scanning rows of holes from a distance. They learned a different way to find the prey. If, subsequently, they sometimes walked around, and sometimes scanned holes from a distance (depending on the prey), then the new tactic would result in switching. If, on the other hand, the birds then always scanned the holes from a distance, the new tactic would increase predation rate permanently, with no switching back and forth.

Another whole class of mechanisms relates to foraging on an even larger scale - where predators look when feeding on prey distributed in patches. A large literature in the field of optimal foraging theory covers this subject (reviews by Stephens and Krebs 1986, Pyke et al. 1977) and shows the various ways in which predators concentrate on larger patches of prey.

6.7 EXPECTATION

Let us consider a series of events that could occur when skunks encounter some prey (a dung beetle (Scarabaeidae), for example) in increasing densities. First, they find some dung beetles. Then, they begin to search for beetles under dung

piles, and their ability to smell the beetles increases (they form OSI's). This happens in a single night, and the skunks remember from one night to the next. Whenever they enter pastures where dung is found, they form these search images. They also change their foraging pattern in such a way as to increase the chance of finding dung beetles. All of these behavioral changes lead to skunks finding dung beetles more readily, but other prey less readily.

I suggest this means that, when skunks begin to find a certain type of food, they subsequently start to 'expect' to find it. They begin to look for it. In the same way, other generalist predators may not look for food in general, but for specific types of food. When doing so, they increase the chance of finding a given prey, but at the same time decrease the chance of finding other types of prey. Perhaps this explains the difference between generalist and specialist predators; that is, both search for a few specific types of prey, but from time to time generalists change the prey they search for, and thus over longer periods of time eat many different types of prey.

It is difficult, if not impossible, to prove that a predator is 'looking for' specific prey. Part of the problem may be that it is difficult to define 'look for' or 'expect', though the meaning is intuitively clear with respect to what people do. For example, red foxes (*Vulpes vulpes*) hunting small mammals walk along trails, with their bodies in a typical 'searching' posture. However, when they search for carrion, they criss-cross small areas of woods, noses lowered to the ground, smelling many different spots on the forest floor (Henry 1975). Is this an example of foxes 'looking for' small mammals versus carrion, or simply foxes using different foraging tactics to find different types of prey?

On the other hand, an example that clearly illustrates the concept of 'looking for' prey is predation by hyenas on African ungulates (Kruuk 1972). When spotted

hyenas (Crocuta crocuta) hunt wildebeest (Connochaetes taurinus) or Thomson's gazelle (Gazella thomsoni), their packs consist of 1.2 to 1.4 animals. However, when they hunt zebra (Equus burchelli), their packs may increase to 27 animals, with a mean size of 10.8. While assembling to hunt zebra, hyena clan members engage in quite a different and more excited ritual of 'greeting' than at other times. And, when actually hunting zebra, they bypass hundreds of wildebeest and other non-zebra prey. When the hyenas look for a certain type of prey, they rarely choose others.

6.8 DENSITY-DEPENDENT PREDATION

The above examples from the literature show that many predators are capable of switching among prey. However, they report only one switching mechanism for each predator. My results show that skunks use several switching mechanisms. This does not mean that skunks are different from other generalist predators; rather, I suggest that researchers have not found more than one switching mechanism per predator because they have not looked for more. Since other animals provide examples of most of the switching mechanisms that skunks use, I also suggest that most generalist predators have many mechanisms by which they can switch among prey.

I do not mean to imply that all generalist predators switch; rather, I suggest that prey switching by generalist predators is so common that we should assume a priori that a generalist switches unless information to the contrary is available. If we do so, then we should also a priori assume that such a generalist exerts density-dependent predation on its prey, since the increase in probability of finding prey due to switching can be quite large. For example, in my long-term search image experiments, skunks increased the distance at which they could detect prey from 10 to 30 times. At the start of the first feeding session, the skunks detected dogfood at 0.5m and dummy nests at about 2m; by the end of the last feeding session, skunks

detected dogfood at 15m and eggs at about 25m. Such large increases in the probability of finding prey may result in large increases in predation rate, and thus very strong density-dependent predation.

6.9 PREDATOR DIETS IN THE WILD

Showing that predators use various switching mechanisms to find prey is far removed from the end result - predators eating prey in the wild. If generalist predators do use these switching behaviors, we should see, from their diet, that they change prey selection through time. Even if we cannot track selection through time, we should still see the following features that correlate with switching (Murdoch and Oaten 1975): 1. If prey selection at equal prey densities is strong and consistent among individual predators, then they do not switch. 2. If prey selection at equal prey densities is weak overall and consistently weak among individual predators, then they do not switch. 3. If prey selection at equal prey densities is weak overall, but strong and variable among individual predators, then they do switch. Basically, if diets vary among individual predators, then we may guess that diets also vary through time in response to changes in the relative frequency of different prey species; that is, switching may be common where diets are variable.

However, studies of food habits rarely show these features. This happens not because switching mechanisms are not strong enough or do not occur in the wild, but because we cannot easily measure selection in the wild. To do so ideally, we must follow individual predators through time to see the exact sequence of foods eaten, while at the same time measuring prey availability. This is a very difficult task and is a problem in technique, not in the concept of switching.

In reality, people usually estimate prey selection by analyzing contents of scats or stomachs. Scat analysis has problems in identifying scats and scat age, and stomach analysis has the problem of measuring predation sequences. To date, there

is no way to identify which individual a scat comes from, although the possibilities can occasionally be narrowed to a few individuals. Even the species (let alone the individual) that scats came from can be difficult to discern. For example, Pearson (1966) was forced to treat scats from feral cats, raccoons (Procyon lotor), gray foxes (Urocyon cinereoargenteus), striped and spotted skunks (Spilogale gracilis), and opossums (Didelphus virginianus) as coming from a 'typical' predator. Such problems with scat analysis create a major setback to the recognition of switching behaviors, for even when feeding data from different individuals (let alone different species) are combined, changes in selection can be lost; different individuals do not necessarily switch prey in unison. Analyses of stomach contents also pose problems, for even though both age and individual are known, it is usually impossible to obtain a sequence of prey items from the stomach contents of one individual.

In addition to determining the sequence of foods eaten by a predator, one must also estimate prey availability in order to see if selection occurs. Measurement of real prey densities is in itself a difficult task, but even more difficult is the measurement of relative prey densities since one must often use different techniques to estimate densities of different prey. Such problems with sampling techniques may mask changes in predator diets due to switching, and until these problems have been solved, food habit studies cannot be used to measure even selection, let alone switching.

6.10 FIELD POPULATION STUDIES

Although switching behavior is interesting in itself, its importance lies in its effects on population dynamics. Simply because predators switch among prey does not mean that they regulate prey densities (Taylor 1984). To see how predators that switch affect prey populations in the real world, we must look at field studies of population dynamics.

Early studies of population dynamics were limited by the current state of theory and by limitations of the study organisms. Lotka-Volterra equations gave a theoretical understanding of predation; however, these equations assumed that only the numbers of predators were important, not the numbers of prey eaten by each predator. Most of the major ideas and tests in population dynamics came from small mammals (Krebs 1979); however, predation on small mammals could not then be measured directly. Consequently, it was assumed that measuring changes in numbers of predators was sufficient to measure changes in predation rate. When no correlation was found between the two, it was concluded that predators do not affect small mammal populations. This conclusion was often not retested when theoreticians found that predation rate per predator is important. For example, Christian (1950) developed the idea that stress causes population reduction at high densities. He studied populations of Microtus pennsylvanicus and subjectively estimated numbers of foxes, hawks and weasels. He concluded that predator immigration lags behind development of peak densities of Microtus, and so predation could not be important (in other words, only numbers of predators are important). He missed the potential effect of a functional response, especially for the generalist predators, foxes and hawks.

On the other hand, it has been possible to measure predation rate directly with some other animals, precluding the need to assume whether numerical or functional response is more important. In some such cases it has long been known that predators affect prey populations. For example, predation rate on nests of ground-nesting birds is easy to measure directly, and most studies have shown that nest predation is high. Keith (1961, p80) found that nest loss in mallard ducks was 64%, and said that "few studies in recent years have failed to show that predators were the chief cause of nest loss".

After the importance of the functional response was first stressed by Holling in the mid-1960's, researchers began to estimate predation rate by each individual predator. Pearson (1964, 1966, 1971) live-trapped three species of small mammals (meadow voles, harvest mice (Reithrodontomys megalotis) and house mice (Mus musculus)) and collected scats from various terrestrial predators. He estimated the numbers of predators from the number of scats, then the number of prey killed per predator, prey selection, and predation rate. He concluded that predators did not affect vole populations at the peak of the cycle, but that they retarded recovery of populations. Predators supplemented their diet when vole numbers were low, but secondary prey could support very few predators, and so predator density dropped a few months after the vole crash.

Pearson's explanation fits the idea of prey switching by generalist predators, introduced by Murdoch and Oaten (1975). At low to medium vole densities, predators exerted density-dependent predation by switching, and retarded recovery of prey populations. At high vole densities, the functional response of predators leveled off and prey then escaped the effects of predation. Such predators acted partially like specialists in that alternative prey could not support the predator population for long.

Predators that are inherently generalists may act as complete specialists when alternative prey are absent. For example, in the Canadian arctic, arctic foxes (Alopex lagopus) prey upon brown lemmings (Lemmus sibiricus). Although foxes may be able to catch other types of prey, there are no other prey species available in that size range. Therefore, lemming populations are not regulated as a result of prey switching by foxes (Krebs 1964, Pitelka et al. 1955); rather, the foxes act as specialists.

Conversely, the greater the density of alternative prey, the greater the effect

switching has on prey populations. Erlinge et al. (1983) studied noncycling populations of field voles (Microtus agrestis) and wood mice (Apodemus sylvaticus) in an area where there was an abundant supply of alternative prey - of the total prey biomass, 50% was rabbits. The researchers collected scats and counted numbers of 6 generalist and 4 specialist predators. The generalists changed diet in relation to changes in prey numbers (with a 2-3 month lag), and these changes in diet were much greater than changes in predator numbers - i.e. the predators switched. Erlinge et al. (1983, 1984) suggested that predator populations did not fluctuate with vole and mouse populations because of the abundant supply of alternative prey. Predator populations were high enough so that when vole and mouse populations increased, predation could increase simply by individual predators switching to these small mammals.

Although the explanations for the results in these studies are convincing, the studies are descriptive. It is possible that predation rates responded to but did not affect prey densities. Predation may be compensatory - that is, in the absence of predators, some other mortality factor may account for the prey that predators would normally kill. Even if predation is not compensatory, switching may not be strong enough to affect prey densities. Experimental studies are necessary.

Lately, biologists have begun to experimentally manipulate densities of both predators and alternative prey. For example, Erlinge (1985) excluded avian and mammalian predators from an enclosed area of 0.5 ha, yet allowed field voles (Microtus agrestis) to move freely in and out. Vole populations declined less in the experimental area than in two control areas during the non-breeding season. However, by the end of the breeding season, vole numbers on all areas had equalized. Thus, predation was significant only during the non-breeding season. Because voles could move freely, there is no way of knowing whether other sources

of mortality during the breeding season compensated for the lower level of predation, or whether dispersing juvenile voles immigrated more to the predator removal area.

Taitt and Krebs (1983) found more conclusive results. They studied the decline in population density of Microtus townsendii in spring. In different areas, Taitt and Krebs added cover (protection from predators), reduced cover, added food and placed nets over areas to reduce predation. They found that, in the first 6-week period, vole populations protected from predators survived better than others, but not in the second 4-week period. The first 6-week period of the spring decline was the result of predation, while the last 4-week period was the result of dispersal.

However, not only might predation in general be compensatory, but predation by one type of predator might be compensatory - that is, other predators might increase predation if that one is removed. For example, Greenwood (1986) removed only striped skunks from prairie uplands. In areas where there were no other main predators, nesting success of upland ducks increased from 5% to 15%, but in areas where there were red foxes and Franklin's ground squirrels (Spermophilus franklinii), nesting success did not increase. Red fox and ground squirrels compensated for skunk predation. This shows that alternative predators affect the importance of a given predator in regulating prey populations. It is not just one species of predator that regulates prey numbers, but all the generalists together.

These studies manipulated predation pressure and showed that often predation is not compensatory. However, to see how important switching is, populations of alternative prey should be manipulated. Various studies have shown that additions of alternative food often decrease predation on the main prey. For example, Lindström et al. (1987) added supplementary food (commercial dogfood

and deer carcasses; predators were mainly red foxes) to an area, then measured grouse (Capercaillie, Tetrao urogallus; black grouse, T. tetrix; and hazelhen Bonasa bonasia) populations in that area and in a control. More juvenile grouse survived in the predator food addition areas (0% of the population in the control was juvenile, compared to 33% in the experimental areas).

Most such studies show that predation decreases when alternative food is added, but Crabtree (1984) showed how this actually happens in one case - i.e. what mechanisms are used to switch. He studied predation by striped skunks on duck nests, and added supplementary food (dead fish and dogfood) to one area and kept another as a control. In June, the added food increased nest survival and skunks spent less time in nesting areas. However, in July, the added food did not increase nest survival. Adding an alternative food item decreased predation on nests, but only during part of the year. Crabtree noticed that in June, skunks walked around while looking for food, but in July, they shifted to a sit-and-wait foraging mode for feeding on mobile insects and small mammals. Skunks had already switched off nests in July, and so the alternative food had no additional effect. In other words, in June skunks typically searched for nests, but in July another prey increased in density, causing skunks to switch off nests. This is a good example of a predator 'looking for' certain types of prey, and then switching to 'look for' others when others increase in density.

7. CONCLUSIONS

The evidence suggests that prey switching is the norm for generalist predators. I found many different mechanisms for prey switching in striped skunks, and there are many other examples of switching mechanisms in other generalist predators. Therefore if alternative prey are available, generalist predators should

switch selection, exert density-dependent predation and regulate prey to some degree.

Theory shows how various properties of prey and predators affect stability. Different types of functional responses (how changes in prey density affect number of prey eaten per predator) can affect regulation of prey populations in various ways. Predators with a type 3 functional response (S-shaped) tend to regulate prey at low prey densities, and one of the few ways that predators can show a strong type 3 functional response is by switching.

Much of the controversy and disagreement over the effects of predators comes from too few good field studies. There is much theory chasing little experimental evidence. In the most recent edition of his ecology textbook, Krebs (1985) concludes that "This assumption [that predators determine abundance of prey] can be tested by predator-removal experiments, but few have been properly done on field populations." Sih et al. (1985, p 283) reviewed the literature on experimental tests of predation and suggested that "Virtually every report of experimental field studies on predation showed some significant effects." In other words, there are few good studies of predation, but most of those do show that predators in some way affect prey abundance.

Switching has not been given enough importance in population dynamics studies. Perhaps when we encounter a new system that has generalist predators and alternative prey, the onus should be on biologists to prove that the predators do not regulate prey, rather than to prove that they do.

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APPENDIX 1. Estimating variance of a parameter from several samples.

Suppose we have estimated a parameter (m_i) and its variance (v_i) from a series of groups. We want to estimate the variance of the overall mean of the parameter estimates from all groups. I suggest that when there are significant differences among the groups, then the best estimate for the variance of the grand mean is obtained by simply using the individual parameters and estimating the variance among them, ignoring their individual variance estimates. If there are no significant differences among the groups, then the best estimate for variance of the grand mean is one that takes into account both the variation within and among groups, treating all data as belonging to one large sample combined. A third possibility, using only the individual parameter variances and disregarding variation among the parameters is never as good as the other two.

As an example, I will consider the case in which m_i are means of a group, and thus v_i are the standard errors squared. For simplification, let sample sizes, n , be the same for all groups. Then the grand mean, M , is simply the mean of the individual m_i .

The three ways to estimate the variance of the grand mean are:

- 1) Using only among-group variation, and ignoring within-group variation, v_i .

$$V_1 = \frac{1}{N(N-1)} \sum (m_i - M)^2 \quad (1)$$

- 2) Using only within-group variation, v_i , and ignoring among-group variation.

$$V_2 = \text{var}\left(\frac{1}{n} \sum m_i\right)$$

$$= \frac{1}{n} \sum v_i = \frac{1}{N^2 n(n-1)} \sum (\sum x_{ij}^2 - nm_i^2) \quad (2)$$

3) Using both within- and among-group variation, treating all data as belonging to one large sample combined.

$$V_3 = \frac{1}{Nn(Nn-1)} \sum \sum (x_{ij} - M)^2 \quad (3)$$

x_{ij} = individual observations from groups

An ANOVA can be used to analyze differences among the m_i , with the following summary:

Source of Variation	D.F.	Sum of Squares	Mean Square	
Among groups	$N-1$	$\frac{n}{N} \sum m_i^2 - \frac{n}{N} (\sum m_i)^2$	$\frac{SS_{among}}{N-1}$	(4)

Error	$N(n-1)$	$\sum (\sum x_{ij}^2 - nm_i^2)$	$\frac{SS_{error}}{N(n-1)}$	(5)
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Total	$Nn-1$	$\sum \sum x_{ij}^2 - \frac{1}{Nn} (\sum \sum x_{ij})^2$	$\frac{SS_{total}}{Nn-1}$	(6)
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With a little bit of algebra, (1) and (4), (2) and (5), and (3) and (6) can be compared to show that

$$V_1 = \frac{MS_{among}}{Nn}, \quad V_2 = \frac{MS_{error}}{Nn} \quad \text{and} \quad V_3 = \frac{MS_{total}}{Nn}.$$

Thus the three variance estimates correspond to the three MS estimates.

If there is a significant difference among groups, then

$$F = \frac{MS_{\text{among}}}{MS_{\text{error}}} > 1, MS_{\text{among}} > MS_{\text{error}}, \text{ and } V_1 > V_2.$$

Also, since MS_{total} is a weighted mean of MS_{error} and MS_{among} , it will always be between MS_{error} and MS_{among} in value. Thus $V_1 > V_3 > V_2$, and V_1 is the largest estimate for the variance of the overall mean. If we use it as our estimate of variance, then our test of significance will be most conservative. A significant difference among groups means that they do not come from the same population and estimating overall variance using V_2 or V_3 would include the smaller within-group error estimates.

If there is no significant difference among groups, then the groups can be considered to come from the same population, and the best estimate for the variance is V_3 , which considers all groups together.

This reasoning can also be shown to hold if m_i are not just means, but any parameter estimates that are normally distributed.

APPENDIX 2. Jackknife estimation of variance of S, the measure of microhabitat selection.

Many estimates of parameters are not normally distributed, and even more of them do not have simple variance estimates. The jackknife procedure is a way of normalizing estimates of parameters and of estimating their variances. I will first describe the general technique (Miller 1974) and then derive a variance estimate for the microhabitat selection index, S.

If we let:

E = an estimate of some parameter based on sample size n

E_{-i} = the estimate of E based on sample size $n-1$, with the i^{th} observation deleted,

$$E_i = nE - (n-1) E_{-i} \quad ; i = 1, \dots, n \quad (1)$$

Then E_i will be (under certain conditions) normally distributed, and thus the jackknife estimate for E is simply the mean of E_i ,

$$E_M = \frac{1}{n} (\sum E_i) \quad (2)$$

and the variance of the mean is the standard error²,

$$\text{Var}(E_M) = \frac{1}{n(n-1)} \sum (E_i - E_M)^2, \quad (3)$$

The conditions I referred to above are that E be estimated from a sample of independent and identically distributed random variables (of any distribution, not just normal) and that the parameter estimate be of a certain general type. One allowable form of parameter estimate is any function of the mean of the observations.

S , the index of microhabitat selection I use, satisfies these requirements. If we consider an individual observation to be a microhabitat choice, with 0 for microhabitat A and 1 for microhabitat B, then S is a function of the mean of these individual observations. These observations are independent if we assume that microhabitat choice is independent of the previous one chosen.

The jackknife estimate of S , S_M , and its variance result in a simple form.

Let: A = number of microhabitat A chosen

B = number of microhabitat B chosen

S_{-i} = S estimated with a microhabitat type i choice deleted

$$S_A = nS - (n-1) S_{-A}$$

$$S_B = nS - (n-1) S_{-B}$$

No matter which observation is deleted, S_{-i} will take on only two possible values, S_A or S_B , and therefore S_i (from eq. (1)) will take on the value of S_A A times and S_B B times. Thus, from eq. (2),

$$S_M = \frac{1}{n} \sum S_i = \frac{1}{n} (A S_A + B S_B) \quad (4)$$

To find the $\text{var}(S_M)$ we note that since S_i can only take one of two values, it is a binomial variable. The variance of a binomial that can take on values of only 0 or 1 is known, so we transform S_i so that

$$X = \frac{(S_i - S_A)}{(S_B - S_A)} \quad (5)$$

and X will be either 0 (when $S_i = S_A$) or 1 (when $S_i = S_B$). X is a binomial variable, and therefore

$$\text{Var}(X) = \frac{AB}{N^3} \quad (6)$$

If we rearrange (5) and take the mean, then we get that

$$S_M = (S_B - S_A)X + S_A \quad (7)$$

$$\text{and therefore} \quad \text{Var}(S_M) = (S_B - S_A)^2 \text{Var}(X) \quad (8)$$

$$= (S_B - S_A)^2 \frac{AB}{N^3} \quad (9)$$

So for an estimate of S we use (4) and for the estimate's variance, we use (9).

For large sample sizes S_M will be normally distributed, and for small sample sizes

$\frac{S_M}{\sqrt{\text{Var}(S_M)}}$ will be distributed with the t-distribution.

APPENDIX 3. Fitting an asymptotic equation to detection distance data.

I estimated reaction distance at any prey item number by fitting an asymptotic equation to the data. I used an asymptotic equation because in many of the trials reaction distance seemed to level off (Fig 4 example plots), and also because it is a biologically reasonable assumption. It does not seem reasonable that skunks increase reaction distance infinitely.

I used a variation of an equation called the 'disc equation' (Holling 1959). The disc equation is given by

$$Y = \frac{A X}{1 + B X} \quad (1)$$

where Y = reaction distance
 X = prey sequence number
 A, B = parameters

There are two problems with this equation. One is that it assumes that initial reaction distance is 0. Another is that if the data for X, Y form a straight line then both A and B equal infinity, and the equation breaks down. Therefore I used the following variation of the disc equation:

$$Y = \frac{X}{\frac{1}{E} + \frac{X}{A}} + C \quad (2)$$

where C, A, E are parameters that represent:
 C : initial reaction distance
 A : increase from initial reaction distance to maximum

(asymptotic) reaction distance

E: initial rate of increase of Y (slope).

If the data form a straight line, then A disappears from the equation and it simplifies to the straight line equation

$$Y = E X + C \quad (3)$$

where E is the slope of the line and C is the initial distance.

I fitted equation (2) using a nonlinear estimation procedure (Dixon et al. 1986), because it is not possible to put the equation in a form in which linear estimation could be used. The nonlinear estimation procedure uses a maximum likelihood iteration technique - it calculates how well an equation given by a set of values for A,C,E fits the data, and by trying different sets of values, the procedure finds the set with the best fit. The procedure needs an initial set of values that are close in value to the final set, so I wrote a computer program that would allow me to find a range of values for the parameters within which the ones with the best fit lie.

The nonlinear estimation procedure gave estimates for A,C,E, for the reaction distance at any X, and variances of these. When E was large, then the variance was correlated with the mean, and I used the arctan transform to normalize the estimate. Arctan(E) is the angle of the initial slope. I used all these estimates in further analyses.

The main flaw in using the parameter estimates is a flaw common to all regression analyses. The variance of each parameter estimate is not independent of the other parameters. For example, the variance of A is the variance with C and E held constant. When A is correlated with C or E then variance is underestimated.

This problem was minimized when calculating the means of parameters over several trials. If there were no significant differences in parameter values among the

trials, then among-parameter variance was equal to the individual parameter variances, and thus the individual variances did represent good estimates of variance. If there was a significant difference among trials then I measured variance of the overall mean by using the among-trial variation (Appendix 1), and disregarded the individual, biased, variance estimates.

In some of the trials the best estimate for A was infinity. When this happened I classified A as unknown, rather than as infinity, because the variance was so large that the confidence intervals usually ran from 0 to infinity. In other words, the maximum reaction distance was not infinity, but rather the data were too scattered to give a good estimate for A.