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Density-dependent predation by skunks using olfactory search images

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Abstract The formation of search images can create density-dependent predation. Predators have been shown to form search images when searching for many small prey items in one feeding session. This paper reports experiments that test whether striped skunks can form olfactory search images in other situations: when prey are found over several days, when prey are large, and when prey are found in certain habitats. Striped skunks were raised in captivity, and their reaction distance to food was measured outside in a natural grassy area. In experiment 1 skunks were offered many small food items for several days in a row. From one day to the next, skunks initially detected food from further away, they increased detection distance faster and their maximum detection distance increased – i.e., they formed olfactory search images faster and stronger from one day to the next. In experiment 2 skunks formed search images over several days when finding only one large food item per day. In experiment 3 skunks lost olfactory search images when they entered habitats in which they had previously searched for another type of food. These long-term search images magnify the effects of short-term search images, extend the effects of short-term search image to longer time spans, and affect different species from short-term search images.

Key words Search image · Skunks · Foraging · Density dependence · Olfaction

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Introduction

Population regulation by predators only occurs with some form of density-dependent predation. There are many behavioral mechanisms for this. For example, after finding several of one prey type, the predator may: restrict the area of search (Stephens and Krebs 1986) or search slower (Gendron and Staddon 1983; Guilford and Dawkins 1987) and thus find more prey that are patchily distributed, learn to look in those types of microhabitats that the prey are found in (Royama 1970), change hunting strategy (Sugden and Beyersbergen 1986), or form search images (Tinbergen 1960; Gendron 1986; Guilford and Dawkins 1987).

Many of these mechanisms of density dependence are mediated through the spatial and temporal heterogeneity of the prey. For example, when prey live in patches, then a predator that slows foraging speed or turns more frequently after finding prey will tend to stay in that prey patch. This will lead to higher predation rate at higher prey densities.

Search images are also dependent on prey heterogeneity. Predators form search images by increasing their ability to detect a specific prey type. Work on search images has considered their formation after the predator has fed on many small food items during one feeding session (Dawkins 1971a; Gendron 1986; Lawrence 1986). This is also applicable to food that is aggregated over short time scales, for example birds feeding in a patch of insects.

However, in nature, patterns in prey distribution are more complex than patches of small prey that are found only in one feeding session. For example, food is often aggregated over longer time scales than just one feeding session of the predator. It would be advantageous for predators to be able to retain their search image from one feeding session to the next, to benefit from this longer time scale of patchiness. In addition, prey are usually found in certain habitats – it would also be advantageous for predators to use this information in developing their search images.

Finally, typical search image experiments have concentrated on many small prey items. In nature, many predators also feed on larger prey items, which are only found once or twice during a feeding session. It would be advantageous for predators to be able to form search images of food that they find once per feeding session.

In the past it has been difficult to show that predators form search images because it is almost impossible to separate the formation of search images from simply searching at a slower rate (Guilford and Dawkins 1987). These two have different effects on prey populations: if a predator reacts to increasing abundance of a prey type by searching more slowly, then predation risk would increase for all prey types in that area. However, if a predator forms search images then it would switch away from other prey in that area.

In previous work I showed that striped skunks (*Mephitis mephitis*) form the olfactory analogue to visual search images (Nams 1991). The methodological problems of proving the existence of search images are avoided with olfactory search images. Skunks increase their ability to detect prey as a result of finding prey by the sense of smell, independently of changes in searching speed. Furthermore, search images of different senses interacted with each other – i.e., skunks focused on formation of search images with one sense at a time.

In the previous study I showed that skunks form olfactory search images when finding many small food items over a short period of time. In this study I extend this work to investigate whether striped skunks can retain search images over several feeding sessions and days, whether they can form search images when feeding on large food items that are found only once per feeding session, and whether search images can be associated with habitat types.

General methods

Striped skunks are nocturnal, generalist predators that find prey mainly by smell and sound. They feed upon many types of foods with many different sizes and distributions; insects and berries are small and encountered many times during one feeding session, but duck eggs, small mammals and carrion are large enough to satiate skunks in one feeding session (Crabtree 1984; Rosatte 1985). Most foods are patchily distributed, with patches large enough and lasting long enough so that skunks find them night after night, not just during one feeding session.

I used the same methods as reported in Nams (1991). The general procedure was to measure the distances at which semi-tame skunks reacted to a series of food items in an outdoor grassy area. Skunks react very noticeably to the smell of food, pointing their noses high into the air and walking in a straight line towards the food item. The point at which they react to the smell of food is very abrupt and obvious, and it is easy to measure the distance between that point and the food item (Nams 1991). For each piece of food I measured the distance between the point at which the skunks reacted to the odor and the food item (the "reaction distance"). This procedure was repeated many times, with various types of food items, as specified in the following experiments. One trial consisted of measuring reaction distances to a series of food items for one animal.

In each trial the reaction distance either increased linearly or increased and then leveled off. To describe the change in reaction distance, I fitted an asymptotic equation to the data from each trial.

I used a variation of the disc equation (Holling 1961), given by:

$$\text{Distance} = \frac{\text{Prey}\, n}{\frac{1}{S} + \text{Prey}\, n / D_M - D_I} + D_I \qquad (1)$$

where D_I, D_M, S are parameters that represent (Fig. 1):

D_I = initial reaction distance
D_M = maximum (asymptotic) reaction distance
S = initial rate of increase of reaction distance – i.e., the initial slope.

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

$$\text{Distance} = S\ \text{Prey}\, n + D_I \qquad (2)$$

where S is the slope of the line and D_I is the initial distance.

I fitted Eq. 1 using a nonlinear estimation procedure (Dixon et al. 1986). This procedure gave estimates and variances of each parameter, and of the reaction distance at any point in the food sequence. All estimates are listed with their 95% confidence intervals.

For each experiment I did a series of trials with each animal and analyzed the results obtained as follows. I first tested for significant differences among animals, and if not significantly different, then combined data from all animals and did statistical tests on the combined data.

Experiment 1

When prey such as insects are locally abundant, they are often abundant for more than just one feeding session – i.e. more than one night. This experiment tested whether skunks retain search images and increase in their ability to form them when feeding on the same prey over several feeding sessions.

Methods

This experiment is the same as the first part of the reaction distance experiments in Nams (1991), but with the data reanalyzed for long-term effects. In each trial I measured the reaction distance to dry kibble dogfood,

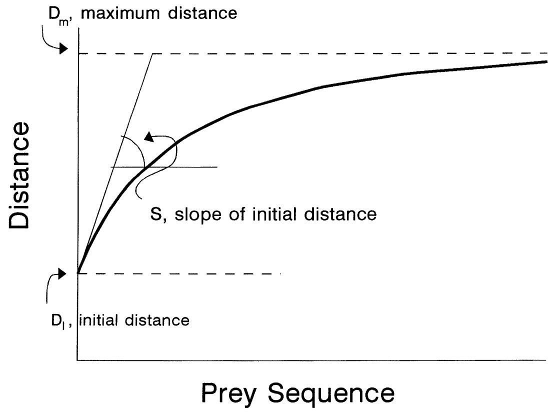

Fig. 1 Meaning of parameters of asymptotic equation that was fitted to reaction distance data

carrying out one trial each day with each animal, for 6–7 days, to see if skunks change how they shift attention onto prey as a result of past trials.

To describe shifts in attention for each trial, I estimated the distance at which skunks reacted to the odor of prey at the start of each trial (D_{I}), their maximum reaction distance (D_{M}), and how quickly they increased reaction distance (S). Then, to see if these increased from one day to the next, I estimated the slope between each parameter estimate and day. Since the parameter estimates had very different variances, I used a weighted regression (weighted by variance^{-1}; Searle 1971; Cochran 1977).

Results

Initial reaction distance

The distance at which the skunks initially reacted to food increased from day to day for skunks 1 and 2, but not for 3 (the slopes of the regression lines differed significantly among individual animals; (Table 1; Fig. 2, 3A).

This regression comparing initial reaction distance used the initial reaction distance estimated from the asymptotic model fitted to the data, but the reaction distances in the last two trials seem more sigmoidal than asymptotic. For these trials, after about two prey items, detection distance increased rapidly – almost an off/on response. This results in an underestimation of initial detection distance.

Therefore; the lack of significance for skunk 3 may have been due to a poor fit of the asymptotic equation, rather than no significant increase. For example, the initial reaction distance estimate on day 7 for skunk 3 is −0.13 m (clearly impossible) yet the skunk detected the first prey item 1.3 m away (Fig. 2). I therefore repeated the regressions, using the actual rather than the estimated reaction distance (D_{I}) to the first prey item. On one hand, this increased random variation because I used information from only one data point per trial, but on the other hand this minimized the problem of a biased D_{I} 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 D_{I}, and there was still a significant difference among slopes for the different individuals (Table 1).

Therefore two of the skunks significantly increased initial detection distance to prey from day to day, and the other did not. 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.

Maximum reaction distance

Maximum reaction distance (D_{M}) increased from day to day for all animals (Fig. 3B), with no significant difference among individual animals (Table 1). Therefore skunks increase the maximum distance at which they react to the odor of prey in the long term.

Initial rate of increase in detection distance(S)

The increase in S from one day to the next was significantly different among individuals, but the increase was significant for each individual (Table 1; Fig 3C). Hence, from one feeding session to the next, skunks shift attention onto prey faster and faster, but at different rates among individuals.

When skunks feed on many small food items, they form search images faster and to a greater degree from

Table 1 Changes in the formation of search images over several feeding sessions. A significantly positive slope means that that parameter increased from one day to the next. All parameters increased, except for the initial detection distances for skunk 3. D_{I} is the initial detection distance estimated from a fitted asymptotic equation (Fig. 1), whereas *Actual initial* is the actual distance that skunks detected the first food item. Slopes are also shown for individual animals whenever animals differ. *Differences among individuals* gives results of *F*-test among slopes of individual skunks (see Fig. 3 for plots of parameters and Fig. 2 for plots of actual detection distances)

Detection distance parameter	Individual animal	Slope	Differences among individuals		
			df	*F*	*df*
Estimated	1	77 (± 51)*	53	4.52^{a}	2,180
initial	2	44 (± 29)*	58		
Distance (D_{I})	3	3 (± 25)	69		
Actual	1	84 (± 37)*	5	10.0^{a}	2,13
initial	2	48 (± 29)*	5		
distance	3	13 (± 25)	6		
Maximum distance ($D_{\mathrm{I}}+D_{\mathrm{M}}$)	All	19 (± 47)*	148	0.62	2,146
Initial	1	0.2 (± 0.04)*	49	6.65^{a}	2,169
rate of	2	0.3 (± 0.07)*	54		
increase (S)	3	0.1 (+ 0.05)*	66		

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

[a] Animals significantly different from each other at $P < 0.05$

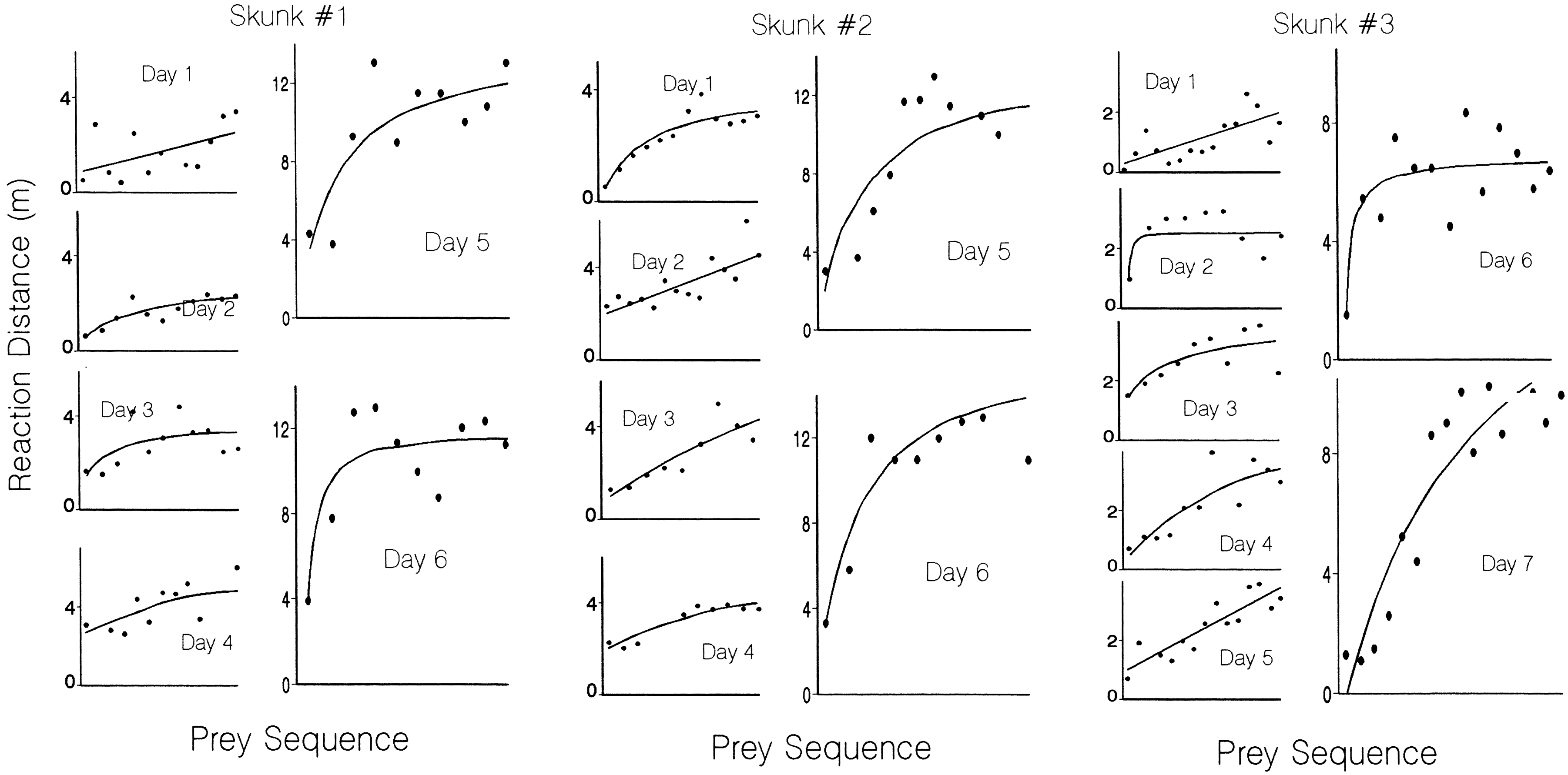

Fig. 2 Reaction distances for each trial for each animal. *Solid lines* represent fitted asymptotic equation

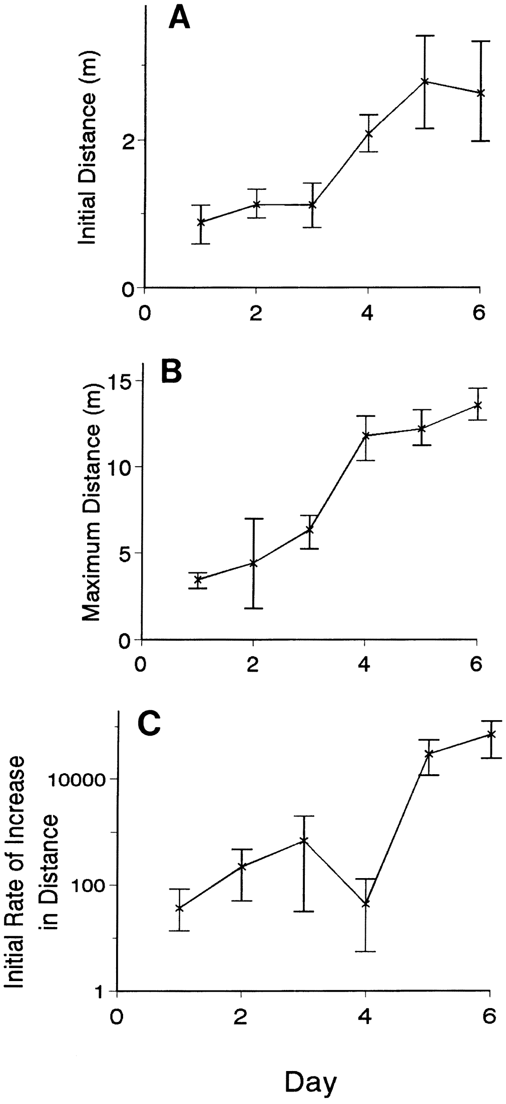

Fig. 3 A–C Search image parameters changed from one day to the next when skunks found the same type of food. Estimates are from parameters of asymptotic equation fitted to reaction distance data

one day to the next. At the start of the first day, the skunks reacted to the odor of food from 0.5 m away, and this increased to 3.4 m by the last day. On the first day reaction distance initially increased by a rate of 0.1 m/prey item, while on the last day reaction distance increased by 2.0 m/prey item. By the last day the increase was so rapid that search images seemed to be switched off/on rather than gradually increased. Finally, on the first day reaction distance reached a maximum of 3.4 m, while on the last day it was 14.3 m.

Skunks could not only retain, but also enhance the effects of short-term search images over several feeding sessions. Formation of short-term search images allowed skunks to increase reaction distance from 0.5 m to 3.4 m – a 7-fold increase. Formation of long-term search images allowed skunks to increase reaction distance to 14.3 m on the 6th day of the trials – a 10-fold increase above the short-term effects.

Experiment 2

The previous experiment was carried out with small food items. However, in the wild, not all prey are small and abundant. For example, in the spring, skunks feed on eggs of ground-nesting birds. One such nest is usually enough to satiate a skunk (personal observations) since duck or grouse nests can contain up to 14 eggs (Bump et al. 1947; Keith 1961). Skunks generally feed on only one nest per feeding session, often returning to the same area the next night in search of more nests (personal observations). In this experiment I tested whether skunks shift attention to the odor of prey when they encounter only one large food item per feeding session.

Methods

I simulated skunks finding nests of ground-nesting birds on successive nights in the same area – simulated, or dummy, nests have been often used to study nest predation (Major and Kendal 1996). I placed dummy nests on the ground and measured the distance at which skunks reacted to their odor. The general procedure was the same as the previous experiments, except that the prey item was different and just one was used per feeding session.

The dummy nests consisted of four chicken eggs placed on the ground in grass tall enough that they could not be seen from 30 cm away at the eye level of a skunk. Because real nests probably have a much stronger odor than four whole chicken eggs (from feathers, droppings and the bird at the nest), I increased the odor of the dummy nests by poking a 1- to 2-mm hole in each egg. I do not know whether eggs with holes in them released the same amount of odor as a natural nest, but I know that dummy nests with whole eggs released less.

After the skunk found the nest, the animal was allowed to eat them all plus more till 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.

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.

Results

The distance at which each skunk detected nests increased from day to day (Fig. 4), with no significant differences among animals (*F* among slopes of individuals = 0.41, *df* = 2, 13, $P > 0.05$). Thus, even one encounter with a large food item, such as a clutch of eggs, per foraging session is enough to cause skunks to shift

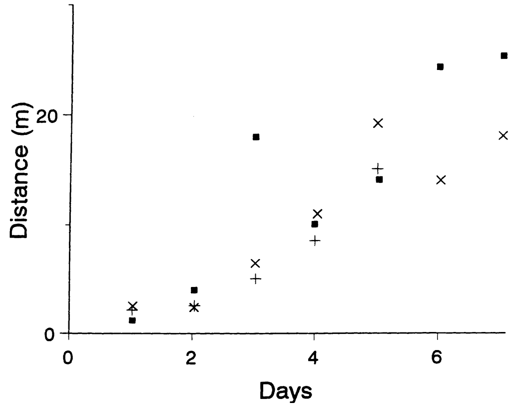

Fig. 4 Detection distance increased from day to day when skunks found only one dummy nest a day. Data shown for each of the three skunks

onto the odor of prey. In just seven daily feeding sessions, skunks increased their reaction distance to dummy nests ten-fold, from an initial distance of about 2.5 m to 25 m.

This increase was not a result of skunks cueing into my odor or other signs from me. From watching the skunks it was obvious that they used the wind; sometimes when following an odor to a nest, if the breeze shifted they would lose the scent. However, although they following scents in the air, they did not follow the scent of my body nor any 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 with their noses up in the air.

Although reaction distance did not level off (Fig. 4), the 25 m distance on the last day may be close to the maximum distance at which skunks can detect food in the wild. At such long distances, slight shifts in wind direction usually caused the animals to lose the scent, and they had to start searching again. Thus this limitation is physical, not physiological; even though the animals might be able to detect much lower levels of odor, the wind causes them to lose the scent.

Experiment 3

Prey not only differ in their odor, but also in their habitat use. Skunks shift attention onto the odor of prey (Nams 1991) and skunks use some habitats more than others (Crabtree 1984; Rosatte 1985). Perhaps skunks can relate olfactory search images to habitat type. That is, when skunks enter a certain habitat, they may already have a search image for the type of prey usually found there, or when they leave a habitat, they may lose the search image of the prey on which they were feeding.

This experiment tested whether an *olfactory* search image formed in a certain habitat is affected by entering another habitat where the animal had previously found a different type of food by *sound*.

Methods

Each trial of the experiment consisted of two acclimation periods and then a test period. In each acclimation period I let the skunks find food 1 in habitat 1 by smell, then food 2 in habitat 2 by sound. In the test period I let the skunks find food 1 in habitat 1 and then the same food in habitat 2. If habitat has no effect on search images then reaction distance to that food should continue to increase in the other habitat.

Foods 1 and 2 were meat and a cooked flour pastry. 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. Habitats 1 and 2 were a well-grazed pasture and a field of flax, about 15 cm tall. I did eight trials, one to four trials per animal. During each trial I presented six to ten pieces of food in each habitat.

If search image is affected by habitat type, then detection distance to food 1 should drop when skunks go from habitat 1 to habitat 2. If search image is dependent only on the last food type eaten, then detection distance should not drop when skunks enter habitat 2 and still find food 1 there.

I fitted the asymptotic equation to the detection distance data to estimate reaction distance at any time. To remove the effect of odors carrying different distances in the two habitats, I then scaled the parameters (Table 2) from the second habitat in each trial by multiplying them by

$$K = \frac{D_{\mathrm{M}}\,(\text{habitat 1})}{D_{\mathrm{M}}\,(\text{habitat 2})} \tag{3}$$

This standardized the estimated maximum reaction distance (D_{M}) to be the same in both habitats.

One problem with this scaling is that it assumes zero variance for K. I estimated var (K Parameter) by K^2 var (Parameter), ignoring the variance of K. This problem

Table 2 Search image × 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 (± $\sqrt{\text{variance}}$)

Individual animal	Trial	K	Last prey sequence no. in habitat 1	Estimated detection distance at last prey sequence in habitat 1
Skunk 1	1	0.827	10	6.70 (± 0.60)
	2	0.927	7	19.6 (± 1.3)
	3	2.12	7	13.4 (± 0.7)
	4	Undefined	7	23.1 (± 1.9)
Skunk 2	1	1.19	7	9.02 (± 0.95)
Skunk 3	1	0.436	7	10.1 (± 0.4)
	2	0.727	6	18.3 (± 1.6)
	3	1.00	7	13.1 (± 0.7)

was minimized because there was no significant differences among animals for any of these parameters; 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 var (Parameter)] were then only used as weighting factors, not as estimates of parameter variances.

Then I estimated how much reaction distance changed when skunks left the first habitat and entered the second one, and the differences in initial distance (D_I) and initial slope (S) between the two habitats.

Results

As soon as skunks entered the second habitat, detection distance for the first dropped from 10 m to 4 m (Fig. 5; Table 3). Not only did detection distance drop, but the initial reaction distance to the first in the second habitat was even lower than at the start of the test period in the first habitat (Table 3). Therefore olfactory search images interact with habitat type.

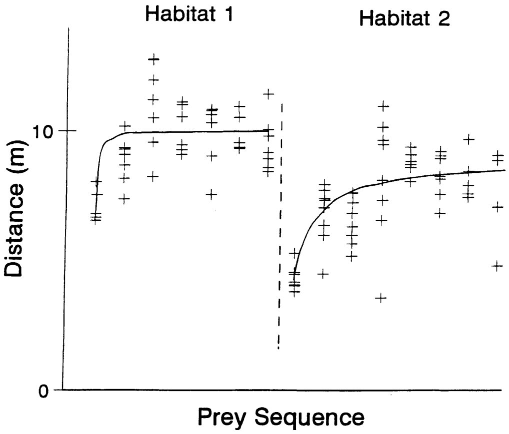

Fig. 5 Search image × habitat interaction: skunks "lost" their search image for one food when they went into another habitat, in which they had been feeding on another food. For the purpose of plotting only, so that data from all trials could be plotted on the same axis, reaction distances in each trial were scaled to the mean parameter values

Table 3 Search image × habitat interaction: skunks formed a new search image for food 1 when they went from habitat 1 to habitat 2. Skunks had previously been entrained to food 1 in habitat 1 and food 2 in habitat 2. *Acclimation* refers to the first of the two acclimation parts carried out in habitat 1. All *df* = 7. See Fig. 5 for plot of detection distances in the two habitats

Change in detection distance parameters from habitat 1 to habitat 2	Mean	95% CI
Detection distance	−7.36	(± 3.2)*
Initial detection distance	−3.86	(± 2.3)*
Initial detection distance from acclimation to hab 2	−0.77	(± 0.18)*
Initial slope	−1.67	(± 4.32)
Initial slope from acclimation to hab 2	−0.30	(± 0.38)

* Significantly different from 0 at $P < 0.05$

Discussion

All of these experiments considered how the reaction distances of skunks to the odor of prey changed under various circumstances. Two different mechanisms can cause reaction distance to change: (1) animals choose to respond at different odor levels, or (2) animals changed in their ability to detect specific odors. In previous work I have shown that skunks do not change prey preference based on experience (Nams 1991), so it is unlikely that skunks chose to respond at different odor levels. Therefore these changes in reaction distance are likely due to changes in the ability to detect different odor levels – i.e. the formation of search images.

With the exception of Lawrence (1985) and Pietrewicz and Kamil (1979), previous experiments on search images only presented prey over short time periods (e.g., Dawkins 1971a,b; Lawrence 1985 1986; Gendron 1986). In both of the former studies birds were presented with small food items over several feeding sessions; the birds formed visual search images faster with experience (Pietrewicz and Kamil 1979; Lawrence 1985). My experiments showed similar results with olfactory search images in skunks. This is further evidence that the shifts in attention of skunks to the odor of specific prey are truly olfactory analogs to visual search images.

Skunks also increased reaction distance to the odor of nests when presented only once during each feeding session. This is the first report of predators forming search images when finding food only once during a feeding session. However, since the experiments did not test for a long-term switching back and forth between different prey types, we cannot rule out the possibility that the animals were learning a new experimental situation. However, experiment 1 did show a decrease in reaction distance from the end of one feeding session to the start of the next, experiment 3 showed switching back and forth on a shorter term, and previous experiments (Nams 1991) also showed switching back and forth on a shorter term. If these other experiments showed that increases in reaction distance were not due to animals learning a new experimental situation, then it is unlikely that the nest experiments did.

The search image and habitat interaction experiment specifically showed that search images were lost when skunks entered a different habitat, one in which they had previously found food by sound. This could happen because: (1) skunks form search images always in association with habitat, independently of previous experience in other habitats, or (2) skunks lost their search image because they had previously fed upon another prey in that habitat. My experiment does not separate between these two explanations.

This experiment answers the question of whether predators can "lose" search images when they enter a new habitat without alternate prey. 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).

Search images have several important ecological effects: (1) they maintain polymorphism in a prey population by selective predation on the more common prey (Allen 1974; Greenwood 1984), (2) they select against aggregated prey spatial distributions, (3) they can stabilize prey populations (May 1973; Murdoch and Oaten 1975), and (4) they constrain foraging behavior in a way not accounted for in optimal foraging theory (McNair 1979, 1980, 1981; Croy and Hughes 1991a,b).

Long-term search images influence these four ecological effects differently than do short-term search images. Long-term search images magnify their effects, they extend the effects to longer time spans, and they affect different species.

The magnification is seen in experiment 1 by the increase in detection distance after six feeding sessions: 10 times greater than at the end of the first feeding session. This results in a higher predation rate on the selected prey, creating a stronger selective force for (1) maintenance of prey polymorphisms and for (2) selection of spatial patterns. It also (3) extends density-dependence to higher prey densities, extending the range of prey densities over which the predator can stabilize prey populations, and (4) even further invalidates the assumption of traditional optimal foraging models that prey detection remains constant.

Long-term search images not only magnify, but also extend the time scale of effects of short-term search images. For predators to be able to form search images, prey have to be aggregated in space or time. Short-term search images require encounters with several of the same type of prey in one feeding session, while long-term search images require encounters over several feeding sessions; thus the minimum size of prey patches has to be larger for long-term search images.

Predators using search images increase predation rate on prey that are aggregated at certain spatial and temporal scales, thus natural selection on prey selects against that scale of aggregation. Larger scaled prey aggregations are selected against by predators that can form long term search images, leading to more dispersed prey distributions or very large aggregations.

Long-term search images also affect different types of prey than do short term search images. Prey not aggregated on a small scale (a small scale is 1 patch ≈ 1 feeding session) will not be affected by short-term search images, nor do short-term search images affect large prey items that are found once per feeding session.

Finally, these longer-term olfactory search images provide a mechanism for the apparent competition observed in nesting birds. For example, Hoi and Winkler (1994) showed that increased density of one type of simulated nest increases predation on another type of nest close by. Olfactory predators would only have to encounter several nests of one type to form a search image, and since this search image is based on the sense of smell, then the predators would more readily find the other type of nest. Although Hoi and Winkler (1994) discounted search images for the increase in predation, this was based on visual search images. Their two nest types looked more different than they smelled.

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