# Foraging Behavior of Ural Owls (*Strix uralensis*) in a Patchy Environment: The Importance of Acquired Information

Kinya NISHIMURA, *Graduate School of Agricultural Science, University of Tsukuba, Ibaraki, 305 Japan*

## Abstract

How the allocation of searching investiment by Ural owls (*Strix uralensis*) in a patchy and fluctuating environment is affected by prior information was experimentally studied. The owls searched among four patches, two with prey and two without prey. During the five days, the positions of two prey patches were randomly assigned daily (random treatment) and for the other five days, they were fixed (fixed treatment). In experiment I, the sequence of treatments was from random to fixed. In experiment II, the sequence of treatments was reversed. The choice of prey present patch was affected by acquired information which owls acquired during one night (short term), a treatment period (medium term), and throughout the experiment run (long term). They predicted the positions of the prey patches, to some extent, in the first choice in one night in the fixed treatment by the experience of previous days. The searching time per visit was also affected by previous information. Owls searched prey patches longer than empty patches. In the random treatment, the giving up time in prey patches was variable, while in the fixed treatment, it was longer and fixed. Although owls could use information on the environment where they had searched to make a decision of foraging behavior, they were not able to choose prey patches accurately. The information which was acquired during the treatment period and throughout the experiment run affected the gain from prey. The changes in gain were not caused by the encounter rate but by the proportion of attack success.

## Introduction

Many theoretical and experimental ecologists have studied foraging behavior as an adaptive response to patterns of resource availability (e.g. Krebs et al., 1974; Krebs et al., 1977; Caraco, 1980; Caraco et al., 1980; Iwasa et al., 1981). Their predictions or interpretations of observed behavior are affected by the kinds of information which foragers are expected to have. For example, does the forager know what kinds of patches there are in an environment, how patches are distributed in an environment, how prey are distributed among patches and whether the distribution patterns and densities of patches and prey are stationary or not? If animals have complete information about these questions and can integrate it, they can forage in the most profitable manner. But animals do not have all this information. They must sample the environment and estimate several parameters in order to exploit re-

sources efficiently. Classical deterministic models of optimal foraging behavior (Charnov, 1976; Orians and Pearson, 1979) did not consider the importance of information acquisition processes. Recently some theoretical studies mentioned the information acquisition problem (Green, 1980, 1984; Iwasa et al., 1981; McNamara, 1982; McNamara and Houston, 1980, 1985). Lima (1983, 1985) performed experiments which concerned an optimal patch sampling process. However, there have been few studies on the sampling process in the foraging behavior of sit and wait foragers (Olive, 1982; Caraco and Gillespie, 1986; Gillespie and Caraco, 1987).

The present paper deals with patch use behavior of the Ural owl (*Strix uralensis*). They mainly hunt small mammals such as voles, mice and mole, in forests and grass lands. They hunt in a sit and wait manner. In a patchy environment, they choose a patch and wait for an encounter with a prey. When they succeed in capturing a prey, they leave the patch with the prey item and handle it in another place (Nishimura, personal observation). Afterwards, they choose a patch and hunt again. In these situations, owls must determine which patch to search and when to leave the patch if they do not encounter prey.

I designed patch choice experiments with owls to study the importance of external information to the prey-searching patterns of owls. I paid special attention to the experience which owls faced during three different time scales; experience during one night (short term experience), experience in a single treatment period (medium term experience), and experience throughout experiment (long term experience). I surveyed the influence of experience during these three time scales on the decisions of patch choice and searching time per visit, and on the gain of prey.

Log linear model analysis was conducted to assess which factors affect the visiting frequency to patches, and an ANOVA was conducted to determine which factors affect the searching time. Furthermore, to survey the variation in response to these factors among individual owls, heterogeneity G value among owls in the factors and F values of mean square of interaction between variation of owls and the factors over mean square of residual were evaluated in the analysis of visiting frequency and searching time, respectively.

## Materials and Methods

### Birds and prey species

The experimental subjects were four hand-raised adult owls, (ID number) 79-A, 84-A, 84-B and 85-A. When the birds were not involved in an experiment, they were kept separately in an aviary and fed liberally on the muscular stomachs of hens.

The prey species was the large Japanese wood mouse (*Apodemus speciosus*). Collecting and maintenance procedures for the mice were similar to those described by Nishimura and Abe (in press).

### Experiments

Owl foraging behavior was observed in a $30 \times 20 \times 12$ m flight cage built in an open field. Owls were observed singly, and kept in the flight cage for the entire course of an experiment. One quarter of the cage was occupied by a grove of coniferous and broad-leaved trees. The owl roosted in this grove during day time. A plan of the flight cage is shown in Nishimura and Abe (in press). At the center of the cage, I set up a mouse enclosure where mice were released (see Fig. 1). The enclosure, $7.2 \times 7.2$ m in area overall but was divided into
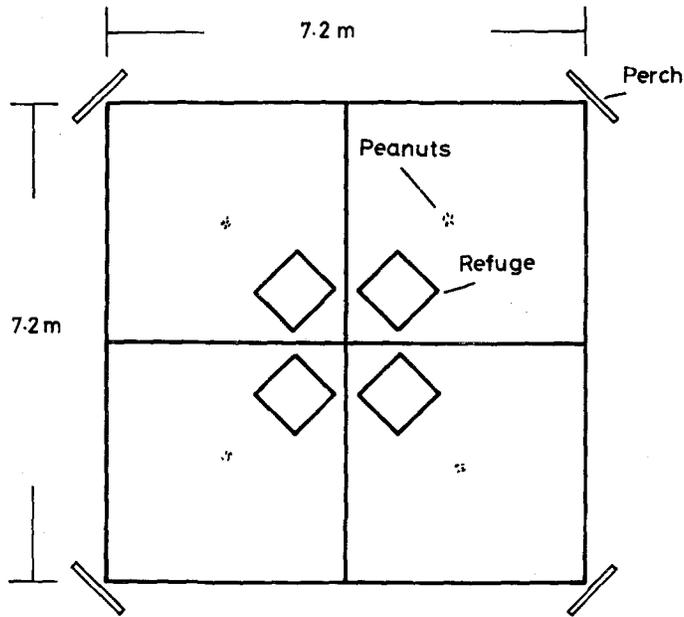
Fig. 1. A plan of the four patch mouse enclosure.

four sections. The enclosure was fenced with steel sheeting 90 cm tall and the floor was covered with soil 2 cm in depth. A refuge for mice was provided in a corner of each section. The refuge was covered with a 90 × 90 cm veneer board, leaving a 3 cm space between the board and the floor. At the opposite corner of refuge, I set a perch 1.6 m high on which an owl could sit and wait for prey. Each perch had an electric switch connected to a pen recorder. When an owl sat on a perch, the identity of the perch and the duration of stay were automatically recorded. Hunting behavior was recorded with a 35 mm still camera triggered by ten pairs of infrared ray switches. The time and section of each attack were recorded automatically, when the owl cut a ray to hunt a mouse in the enclosure. Each section was considered as a patch in which the owl can search from a given perch.

I conducted two experiments. Each experiment consisted of a number of 10 day foraging runs. In both experiments, two patches contained three mice each (prey patches), and the other two patches had no mice (empty patches). A foraging run was divided into two periods of five days. In experiment I, during the first period, prey patches were randomly assigned every day (random treatment period) and during the 2nd period, prey patches were fixed (fixed treatment period). In experiment II, the two treatment periods were assigned in the opposite sequence to experiment I.

At the center of each patch, I put 30 pieces of peanuts as food for the prey mice. Wires prohibited the owl from sitting on the edges of the enclosure, so the owl could search for prey in each patch only while it sat on the associated perch. I recorded every arrival and departure time with or without an attack on a prey in each patch to evaluate the allocation of searching effort among patches.

Owl 85-A was used twice in each experiment. Owl 79-A was used twice in experiment I and once in experiment II. Owls 84-A and 84-B were both used once in experiment I. Because of the unbalanced design, I used GLM procedure in SAS (SAS Institute 1982) for the

analysis of variance. Repetitions of an experiment by the same owl were nested within owls, and owls were considered as a random factor.

# Results

## Visit frequency

### Number of visits to patches in one night

I investigated how the number of visits to patches was affected by four factors; patch types (Pa), experimental treatment periods (Tr), visiting sequence (Vi), and experiment types (Ex). Pa has two levels, patches with prey (prey patch) and patches without prey (empty patches). The levels of Tr indicate whether the treatment was random or fixed. Only the

Table 1. The frequency of visits to patches with some factors which were significant in the log linear model analysis. The factors which were used in the analysis were Pa, Tr, Vi and Ex. Each abbreviated code is explained in the text. Each cell of the marginal tables contains the number of visits pooled all foraging runs. The log linear model ($\ln f = \mathrm{Ex} \times \mathrm{Tr} \times \mathrm{Pa} + \mathrm{Vi} \times \mathrm{Pa} + \mathrm{Pa} + \mathrm{Ex}$) is significant at 0.05 significant level.

I. The analysis of $\mathrm{Ex} \times \mathrm{Tr} \times \mathrm{Pa}$. Test of $\mathrm{Tr} \times \mathrm{Pa}$ with two layers of Ex level and heterogeneity among runs with each experiment.

| Experiments (Ex) | | Experiment I (6)[+] | | Experiment II (3)[+] | |
|---|---|---|---|---|---|
| Patch (Pa) | | Prey | Empty | Prey | Empty |
| Treatments (Tr) | Random | 269 | 187 | 145 | 111 |
| | Fixed | 313 | 131 | 182 | 50 |
| Pooled | | $df = 1$  $G = 13.083$** | | $df = 1$  $G = 26.714$** | |
| Heterogeneity | | $df = 5$  $G = 31.766$** | | $df = 2$  $G = 1.566$ ns | |
| Total | | $df = 6$  $G = 44.849$** | | $df = 3$  $G = 28.280$** | |

[+]The number of runs of experiments. *$p<0.05$, **$p<0.01$.

II. The analysis of $\mathrm{Vi} \times \mathrm{Pa}$ and heterogeneity test over all foraging runs.

| Patch types (Pa) | | Prey | Empty |
|---|---|---|---|
| Visiting sequence (Vi) | First half | 437 | 257 |
| | Last half | 472 | 222 |
| Pooled | | $df = 1$  $G = 4.060$* | |
| Heterogeneity | | $df = 8$  $G = 9.536$ ns | |
| Total | | $df = 9$  $G = 13.596$ ns | |

*$p<0.05$

III. The analysis of Pa and heterogeneity test over all foraging runs.

| Patch types (Pa) | Prey | Empty |
|---|---|---|
| | 907 | 479 |
| Pooled | $df = 1$  $G = 134.352$** | |
| Heterogeneity | $df = 8$  $G = 39.218$** | |
| Total | $df = 9$  $G = 173.570$** | |

**$p<0.01$

IV. The analysis of Ex and heterogeneity test between two individuals which were used in both experiments in common.

| Experiment (Ex) | Experiment I | Experiment II |
|---|---|---|
| | 510 | 486 |
| Pooled | $df = 1$  $G = 0.57837$ ns | |
| Heterogeneity | $df = 1$  $G = 1.52684$ ns | |
| Total | $df = 2$  $G = 2.10521$ ns | |

data on the last three days in each treatment periods were used in the analysis. Visiting sequence (Vi) has two levels (early and late). The patch visiting sequence for each night was divided into the first (early) and last half (late). If the number of patch visits in a night was odd, I omitted the middle visit for that night. The factor Ex consists of two levels, experiments I and II. I also omitted the records of stays with durations less than or equal to 50 seconds.

Using a log-linear model analysis (Fienberg, 1980; Sokal and Rohlf, 1981), I examined the effects of each of these four factors, and also the effects of their first, second, and third order interactions. Following the methodology of Sokal and Rohlf (1981), I tested from the highest order interactions to the single factors. First I tested the pooled data for all runs and then if the factors or the interactions among or between the factors were significant, heterogeneity of these effects were tested among foraging runs by a heterogeneity G-test (Sokal and Rohlf 1981; Zar 1984).

The factors Pa and Ex, and the interactions Vi × Pa and Ex × Pr × Pa were found to significantly improve the fit of the model (Table 1).

*The effect of the second order interaction*: The second order interaction of experiment by treatment by patch type, (Ex × Tr × Pa) was statistically significant (Table 1-I). The effects of this interaction can be made clear by examining the interaction Tr × Pa within each experiment (Ex). In both experiments, the interaction Tr × Pa was statistically significant. The interaction Tr × Pa in experiment I exhibited a heterogenous response among experiment runs. On the other hand, in experiment II the interaction Tr × Pa exhibited no heterogeneity. The ratio of the number of visits to prey patches to that to empty patches was larger in the fixed treatment period than in the random treatment period in the both experiments.

*The effect of the first order interaction*: The first order interaction of visiting sequence by patch types (Vi × Pa) was significant (Table 1-II). The ratio of visits to prey patches to visits to empty patches was larger in the last half (68 %) than in the first half of visits (63 %). The interaction had no significant heterogeneity among experiment runs.

*The effect of the single factors*: The effect of patch types (Pa) was highly significant (Table 1-III). The prey patches were more frequently visited than the empty patches. The factor exhibited a heterogeneity among foraging runs. All foraging runs but one showed a higher proportion of visits to prey patches. The ratio was nearly equal to unity in one case. Thus, the heterogeneity among foraging runs was due to the variation in the magnitude of ratios not to changes in rank order.

The total number of visits to the four patches in the two experiments was compared using a log-linear model (Table 1-IV). Since the number of runs used in experiment I was twice as large as in experiment II, in this analysis, I compared the visit frequency between the two individuals which were used in both experiments, pooling the same number of days' record in each experiment. The pooled data did not significantly deviate from even use of patches and both individual owls exhibited no heterogeneity.

*Auditory cue hypothesis and relative importance of previous days' information*

Since prey patches were visited more frequently than empty patches, there is a possibility that auditory cues associated with the behavior of mice were guiding the owls. To test the

auditory hypothesis, I compared the number of the first visits of each night between patch types in the random treatment period of all foraging runs. In all, owls visited prey patches first 13 times and empty patches first 14 times. These numbers do not significantly deviate from the even proportion expected from a random patch choice ($df = 1$, $G = 0.037$).

To survey the effects of previous days' information on patch choice, I analyzed the number of the first visits using three different factors. The factors were Ex, Tr and Pa. In order to test this issue, I conducted a three way contingency test using a log-linear model. Since I am interested in the difference of the numbers of the first visits between the two patch types and the change of the difference with other factors, only the factor Pa and the interactions between Pa and other factors were analyzed.

The result of log-linear analysis and the contingency table are shown in Table 2. The interaction $Tr \times Pa$ was significant at 0.05. Although the ratio of the number of visits to prey patches to that to empty patches in random treatment period did not significantly deviate from 1.0, the ratio was significantly higher in fixed treatment period. The interaction $Pa \times Ex$ within fixed levels of Tr was marginally significant ($df = 1$, $G = 1.7097$, $p < 0.091$). The proportion of the first visits to prey patches to that to empty patches was higher in experiment II where the fixed treatment preceded the random one, than in experiment I where the random treatment preceded the fixed one.

If owls can acquire and integrate information from their previous experiences, we may expect several patterns of visit to patches.

If owls can retain information on the position of prey among patches, they may visit prey patches more frequently than empty patches. In both treatments, if owls can integrate short term information (within a night), the frequency of visit to prey pataches should increse in the second half of a night's visits, as they gain information about that night's prey distribution. This interaction can be expressed by abbreviated code $Pa \times Vi$ in a log-linear model. During the random treatment period, the information acquired in the previous days is not useful in patch choice, because the positions of prey patches changed randomly every night. On the other hand, in the fixed treatment period, this information is useful in patch choice. Thus, the proportion of visits to prey patches to those to empty patches should be larger in fixed treatment period than in random treatment period. This can be tested by the interaction term $Pa \times Tr$ in a log-linear model. The expected visit frequency may also be affected by the two different experimental designs. In experiment II, the treatment sequence was from the fixed to the random. Thus, if the experience in previous environment affect the decision of patch choice, the frequency of visits in prey patches in the fixed treatment period may be higher than that in the fixed treatment of experiment I which was subsequent to random treatment. This effect is tested by the interaction term $Pa \times Tr \times Ex$ in log-linear model.

The expected patterns mentioned above were supported by observations. Prey patches

Table 2. The test of the numbers of first visit to patches with three factors, Pa, Tr and Ex. The abbreviated codes of factors are explained in the text.

| Patch types (Pa) | Prey | | Empty | |
|---|---|---|---|---|
| Treatments (Tr) | Random | 13 | 14 | |
| | Fixed | 20 | 7 | |
| Pooled | | 33 | 21 | |
| +ln $f$ = Tr × Pa + Ex | | | | |

+The equation shows the model containing significant factors and interaction of factors in log linear model at 0.05 level.

were visited more frequently than empty patches. The choice of prey patches became more accurate in the second half of the searching sequence for a night (Table 1-II). The patterns of visits among Pa and Tr were more complicated. The interaction Tr×Pa with data pooled over the levels of Ex exhibited no significance. But the higher order interaction Ex×Tr×Pa showed significance (Table 1-I). The choice of prey patches was more accurate in the fixed treatment period than in the random treatment period only in experiment II where the fixed period preceded the random period. These results show that the patch choice pattern was affected both by short term information acquired during one night and medium term information acquired during a treatment period and long term information gained throughout an experiment. In the predictable environment (fixed treatment period), the information acquired during each night was available, as well as previous days' information. But the information acquired during the predicatable environment was confused by the experience during the unpredictable environment. This shows that owls probably do not respond immediately to a drastic change from unpredictable (random) to predictable (fixed) environment. This result suggests the possibility that previous foraging experience can affect foraging for more than three days.

Owls did not choose the first patch to visit by auditory cues. Instead, they used information from previous days' experience among patches (Table 2). In the random treatment period, owls could not accurately choose prey patches in the first choice of patch, since the information of previous days was not useful. But in the fixed treatment period, in which owls can use the information of previous days beneficially, owls could accurately choose prey patches in the first patch choice of a night. Furthermore, the accuracy of choosing a patch in the first choice was greater in a predictable environment that did not follow an unpredictable one than it was subsequent to an unpredictable environment.

**Searching time**

*Searching time in one visit*

The mean searching time in a patch per visit was analyzed with five factors by the GLM procedure of SAS (SAS Institute 1982). The factors were individual owls (Ow), repetition of runs with same owl (Re), patch types (Pa), treatment periods (Tr), visiting sequence (Vi), and experiment types (Ex). The repetition (Re) was nested within owls (Ow). Natural logarithmic transformation of searching time was applied to generate normality and homoscedasticity. I focused the analyses on the factors Tr, Pa, Vi, Ex and their interactions. If there were significant interactions with factor Ow with Re nested, it means that these effects or interactions of owls with other factors were heterogeneous among owls.

Table 3 shows the results of ANOVA and the mean log (min.) for each level of the factors which exhibited significant effects on the variation of searching time. The searching time was longer in the fixed than in the random treatment period (Table 3-II-a). Prey patches were searched longer than empty patches (Table 3-II-b). The searching time was shorter in the last than in the first half of visits in the random treatment period (Table 3-II-c). However, in the fixed treatment period, searching time was longer in the last half than in the first half of visits (Table 3-II-c).

*Giving up time in prey patches and empty patches, and the waiting time until attack*

I further examined searching time with factor of prey attack status (Ast). The three levels

Table 3. I. ANOVA table of analysis of searching times in patches with five factors. The abbreviated codes of factors are explained in text. This is a mixed model ANOVA. Factor Ow is random and all others are fixed. The treatment of residual mean squares in the F tests for significance of factors and interactions follows the method of Sokal and Rohlf (1981, p. 285).

| Source factors | df | SS | F-values | |
|---|---|---|---|---|
| Ex | 1 | 0.5446 | 1> | ns |
| Tr | 1 | 4.7580 | 4.76 | * |
| Pa | 1 | 43.9702 | 43.99 | ** |
| Vi | 1 | 0.0018 | 1> | ns |
| Ex×Tr | 1 | 1.9155 | 1.92 | ns |
| Ex×Vi | 1 | 0.8984 | 1> | ns |
| Tr×Vi | 1 | 4.8205 | 4.82 | ** |
| Pa×Vi | 1 | 0.5459 | 1> | ns |
| Ex×Tr×Pa | 1 | 0.9280 | 1> | ns |
| Ex×Tr×Vi | 1 | 0.0533 | 1> | ns |
| Ex×Pa×Vi | 1 | 0.6308 | 1> | ns |
| Vi | 1 | 0.0017 | 1> | ns |
| Vi×Owl | 5 | 25.0280 | 5.01 | * |
| Ex×Pa | 1 | 2.8171 | 1.25 | ns |
| Ex×Pa×Owl | 2 | 4.5231 | 2.26 | ns |
| Tr×Pa | 1 | 1.7559 | 1> | ns |
| Tr×Pa×Owl | 5 | 14.3211 | 2.87 | * |
| Residual | 1458 | 1457.4230 | | |

*$p<0.05$, **$p<0.001$.

II. The means of searching time.

a. Mean searching time (min.) transformed to natural logarithms in two treatments.

| Treatments (Tr) | Random | n | Fixed | n |
|---|---|---|---|---|
| | 1.533 | (726) | 1.659 | (696) |

b. Mean searching time (min.) transformed to natural logarithms in two patch types.

| Patch types (Pa) | Prey | n | Empty | n |
|---|---|---|---|---|
| | 1.729 | (943) | 1.330 | (479) |

c. Mean searching time (min.) transformed to natural logarithms of searching time in two patch types and two visiting sequences.

| Treatment (Tr) | | Random | n | Fixed | n |
|---|---|---|---|---|---|
| Visiting sequence (Vi) | First half | 1.588 | (363) | 1.589 | (348) |
| | Last half | 1.479 | (363) | 1.729 | (348) |

Table 4. ANOVA table of mean searching time among patches of different status (Ast). The factor Ast and the interactions which associated with Ast were analysed. The abbreviated codes of factors are explained in text. This is a mixed model ANOVA. Factor Ow is random and all others are fixed. The treatment of residual mean squares in the F tests for significance of factors and interactions follows the method of Sokal and Rohlf (1981, p. 285).

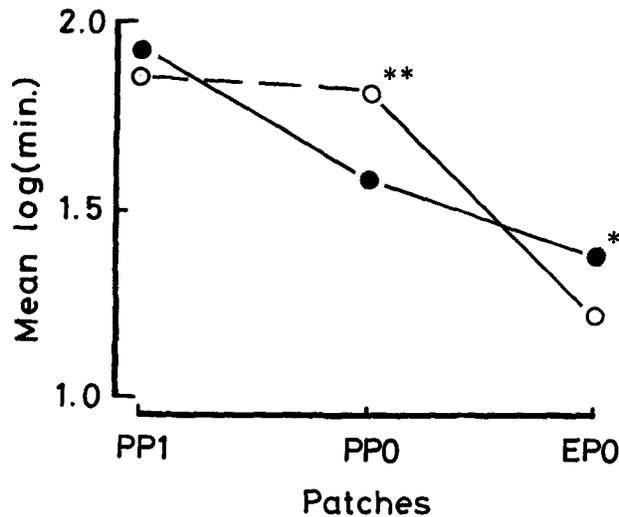| Source factors | df | SS | F-values | |
|---|---|---|---|---|
| Tr×Ast | 2 | 8.4464 | 4.223 | * |
| Ex×Tr×Ast | 2 | 0.2716 | 1> | ns |
| Ast | 2 | 43.4849 | 13.331 | ** |
| Pa×Ow | 10 | 16.3102 | 1.497 | ns |
| Ex×Ast | 2 | 0.7982 | 1> | ns |
| Ex×Ast×Ow | 4 | 10.4217 | 2.605 | * |
| Residual | 1261 | 1373.9366 | | |

*$p<0.05$, **$p<0.01$

**Patches**

Fig. 2. Mean searching time (transformed to natural logarithm) in prey patch ended with attack (PPI), prey patch ended without attack (PP0), and empty patches (EP0). Open circles indicate the mean searching time in fixed treatment period. Solid circles indicate the mean searching time in random treatment period. A solid line connecting circles indicates a significant difference in mean searching times, while a dashed line indicates a lack of significant at $p < 0.05$. ** and * indicate the difference of means between treatments within patch status at $p < 0.01$ and $p < 0.07$, respectively.

of Ast were searching in a prey patch with an attack (PP1) or without an attack (PP0) on a prey, and searching in empty patch (EP0). The mean searching time was tested with factor the Ast (PP1, PP0, EP0) and the interactions between Ast and other factors (Ow, Ex and Tr).

The result of ANOVA is shown in Table 4. The factor Ast was significantly related to searching time. The mean searching time with an attack (PP1) was significantly longer than that without an attack in prey patches (PP0).

The mean searching time in empty patches (EP0) was shorter than in prey patches (PP1, PP0). The interaction Ast × Tr was also significant. The effect of Ast × Tr on mean searching time is shown in Figure 2. In the fixed treatment period, the mean searching time showed no difference between PP1 and PP0, while the mean searching time in empty patches (EP0) was shorter than the other two levels. However in the random treatment period, the mean searching time was longest in PP1, and shortest in EP0. Searching time in a prey patch with an attack (PP1) was not different between the two treatment periods. The searching time in prey patch without an attack (PP0) was significantly longer in the fixed than in the random treatment period, and the time spent in the empty patch (EP0) was longer in the random than in the fixed treatment period.

Thus, not only the number of visits but also the searching time in one visit were affected by previous information. Owls searched in prey patches longer than in empty patches. Apparently, information acquired during a treatment period caused searching time to change. They searched longer in the predictable environment (fixed treatment period) than in the unpredictable environment (random treatment period). The searching time in the last half of a visiting sequence in predictable environment increased. However, the searching time during the last half of visit in unpredictable environment was not different from that during the first half of the visits, although the proportion of visiting numbers in prey patches in-

creased in the last half of the visits relative to that in the first half of the visits. These results show that the decision of searching time in one visit was affected by both short term and relatively long term information. The searching time increased only in the case where owls sampled and got information during one night in the predictable environment. The difference of searching times may reflect not only information known before entering the patch but also encounters with prey in the patch. There are two types of encounter with prey; one in which prey was detected in an area owls could attack, and the other in which prey was in a area where the owl could not attack. If an owl detects prey, but cannot attack, the owl may wait for the prey until it can attack. So posterior information which owls acquired after entering a patch may also affect the searching time.

Giving up time, the time owls take before leaving a patch without attacking prey was longer in prey patches than in empty patches. This means that the owls had different beliefs about the presence of prey in the two patch types. In prey patches, giving up time was longer in the predictable environment than in unpredictable environment. Furthermore, although the statistical test showed only marginal significance, giving up time in empty patches was shorter in the predictable environment than in unpredictable environment. As a result, the difference in giving up times between prey patches and empty patches was larger in the fixed than in the random treatment period. This shows that the owls distinguish patch types more clearly in the predictable environment than in the unpredictable environment. In the fixed treatment period, the mean searching time was not different between searching with and without an attack (give up). But in the random treatment period, in some visits, the owls gave up searching after a short time, and in the other visits, they searched for a long time and encountered a prey. These patterns show that the searching time in prey patches was more variable in the unpredictable environment, but was constant in the predictable environment. If the mean time until prey entered an area where owls could attack was considered to be same in both treatment periods, then the giving up time was variable in the unpredictable environment, and constant in the predictable environment (Fig. 2).

### The number of prey captured and the proportion of successful attacks

The number of attacks per night was compared between experiments and between treatment periods. The number of attacks per night was not different either between experiments or between treatment periods.

I compared the number of mice taken by owls between treatment periods and between experiments. Since the owls took only a few mice in each treatment in an experiment run, I pooled all experiment runs in order to reduce type II error. Owls took more mice in the fixed treatment period (29 mice) than in the random treatment period (16 mice). The difference was marginally significant ($df = 1$, $G = 3.810$, $p < 0.0509$). The number of prey mice taken by owls per night (1.33/day) in experiment II was roughly twice of that in experiment I (0.58 /day) ($df = 1$, $G = 4.0350$, $p < 0.05$).

The proportion of capture success was estimated from the numbers of prey taken by owls and the total attacks. Unfortunately, I could not get complete attack records in several days because of insufficient film exposure by the still camera. Therefore, I only used data from nights with complete records.

To survey which factors affected the proportion of attack success, I carried out a three way contingency test using a log-linear model with three different factors. The factors were experiment type (Ex), treatment period (Tr), and attack type (At). At has two levels, success or failure in attack.

Table 5. The marginal contingency tables of attack frequency in interactions between factor At and other factors which are significant in log linear model analysis. The log linear model is shown to be $\ln f = \mathrm{Ex} \times \mathrm{At} + \mathrm{Tr} \times \mathrm{At} + \mathrm{At}$. The factor At and the interaction $\mathrm{Ex} \times \mathrm{At}$ are significant at 0.01 level. $\mathrm{Tr} \times \mathrm{At}$ is significant at 0.0625.

I. The analysis of Ex At.

| Attack status (At) | | Success | Fail |
|---|---|---|---|
| Experiments (Ex) | I | 9 | 62 |
| | II | 16 | 23 |

II. The analysis of Tr At.

| Attak status (At) | | Success | Fail |
|---|---|---|---|
| Treatment periods (Tr) | Random | 8 | 45 |
| | Fixed | 17 | 40 |

In this analysis only the two interactions (At × Ex, and At × Tr) have any meaning. Table 5 shows the results of log-linear analysis. The interaction Ex × At and the factors At and Ex were significant at the 0.05 level. The interaction Tr × At was significant at 0.0625 level. The proportion of successful attacks was higher in experiment II than in experiment I. It was also higher in the fixed treatment period than in the random treatment period. The overall expected attack success proportion was 0.227.

The owls could catch more prey in the predictable environment than in the unpredictable environment. The degree of predictability in the environment affected the number of mice caught in one night. The owls caught more prey per night in experiment II than in experiment I and in the fixed than in the random treatment period. Since the number of attacks per night was not significantly different between experiments and between the treatment periods, these patterns depended on the difference of the proportion of attack success between treatments and between experiments. This shows that the predictability of the environment affects the proportion of successful attacks.

## Discussion

Many theoretical and experimental studies have been conducted on foraging behavior in a patchy environment. Most works assumed that 1) patches are indistinguishable in appearance, 2) foragers have no cues in advance about which patch has more food available, 3) foragers exploit the same patch only once, and 4) foragers know the distribution pattern of prey among patches (e.g., aggregative or regular) (Krebs et al., 1974; Green, 1980; Iwasa et al., 1981; Hodges, 1985; McNamara and Houston, 1986; Sugimoto et al., 1987). These assumptions were made largely for simplicity in studying the behavior from entering to leaving a patch. Ural owls usually live in a patchy environment and maintain a territory throughout the year, as Southern and Lowe (1968) reported in an allied species, Tawny owl (*Strix aluco*). In a patchy environment, their foraging behavior consists of four components, i.e. patch selection, entering a patch, searching for and handling prey in the patch, and leaving the patch. The assumptions mentioned above are not adequate to study the mechanisms of foraging behavior of Ural owls. These birds exploit some patches more than once. Consequently, if owls use information from previous experience, they will often have cues about which patches are more profitable before they enter any particular patch, and their searching investiment will be influenced by their information acquiring and integrating processes.

Some factors and their interactions in this study can be expected to affect searching in-

vestments, i.e. visit frequency and searching time in one visit, number of attacks, proportion of attack success, and prey taken.

In this study, I categorized three different time scales over which owls acquired information. The information was acquired during one night (short term), during a treatment period (medium term), and throughout a foraging run (long term). During one night, the distribution of prey patches did not change. Whenever owls searched for prey in prey patches, owls had a change to encounter prey, since all mice in one patch were almost never consumed in a night. Therfore, the owls could gain information on the distribution of prey patches during one night. This is information acquired in a short term.

If positions of prey patches are fixed, owls may integrate the information about the distribution of prey patches from the previous days (medium term). However, if the allocation of prey patches changed randomly every night, information about prey patch distribution from the previous days confused their decision making during foraging. Therefore, the owls received different types of information on the distribution of prey patches during each treatment period. The knowledge gained from day to day within a treatment period is considered medium term information. Furthermore, we should also consider the information acquired during a much longer period. The different sequences of two treatments between two experiments were intended to compare the influence of previous long term experience in unpredictable environment on the behavior in the predictable environment.

In foraging in a patchy environment, there are two important steps in the decision process, choosing a patch and deciding to abandon searching in the patch. Information acquired during various durations may influence both these steps. Patch choice changed throughout a night's sampling process, and the owls chose more accurately after sampling the patches. If the environment was predictable, the owls chose a patch in which they had encountered preys in previous days even in the first choice of a patch for a night. However, the accuracy of the first choice in predictable environment decreased when an unpredictable environment had preceded the predictable one. In the fixed treatment period searching time was longer in prey patches and shorter in empty ones than in the random treatment period. Thus, depending on the environmental change, the owls changed their giving up time (Fig. 2).

Even though the owls used information acquired from previous experience, they could not make a completely accurate choice of patch. After a choice of a patch, searching time had great a variability if the environment was unpredictable.

The predictability of the environment affected not only the decisions performed by owls but also the gain of mice. The change in gain did not depend on a difference in the number of attacks, but instead on the proportion of successful attacks. Changes in attack success in different conditions have also been reported by Newman et al., (1988) and Nishimura and Abe (in press). Together with this study, these papers indicate that changes in attack success should also be considered when we try to understand the foraging behavior of animals.

The owl's experiences during three different time scales all affected the patch choice and searching time. Even when owls got valid information during the medium term experience, if owls had faced with uncertainty during the long term, the accuracy of patch choice decreased. This, together with the incomplete fixation of patch choice to prey patches, suggests that in evolutionary time owls have inhabited an uncertain environment in which a sampling process is always needed, but the environment does not change so drastically that previous information is not useful.

In this study, I focused on two steps in the owl decision process while it searches for prey. These decisions were made repeatedly throughout the foraging run. Thus, foraging is a multi-decision process. Each decision step was made using the information gained from previous experience. Theoretical models which can explain this kind of foraging processes must be explored. Some theoreticains have built models of such multiple decision processes using dynamic programming (Houston and McNamara, 1985; McNamara and Houston, 1986; Mangel, 1986; Mangel and Clarck, 1986). But in this case, the information acquiring process may be better modeled as a multiple Bayesian decision process. Theoretical work in multiple Bayesian decision process models which explain the sampling process of information from the environment must be conducted to understand the foraging process of nomadic sit and wait forager such as Ural owls.

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