

Prey susceptibilities, prey utilization and variable attack efficiencies of Ural owls

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Summary. To investigate the factors that influence prey utilization among predators with active prey, three series of experiments were performed in which Ural owls (*Strix uralensis*) searched for and attacked three prey species of wild mice, *Microtus montebelli*, *Apodemus speciosus*, and *A. argenteus*, in a large flight cage. Over the whole study, owls attacked mice about ten times a night. The number of attacks on each prey species did not differ from that predicted by a random attack model. *M. montebelli* was taken more than either *Apodemus* species. Prey utilization appears to be influenced by prey susceptibilities only and it is unlikely that prey selection by the owls affected prey utilization patterns. Under the experimental conditions, random attack is predicted by optimal foraging theory. However, random attack may be explained just as well by the inability of the owl to discriminate prey type. The owls, energy gain was adjusted not by alteration in the number of attacks on a prey species but rather by alteration in the capture success between experiments. Capture success increased in poor food conditions for the same prey species. This flexibility in capture success has not been considered in the assumptions of optimal foraging theory. In conventional optimal foraging theory, the probability of capture success is implicitly assumed as constant and unity. We suggest that this assumption is inadequate to understand the foraging behavior of owls.

Key words: Ural owl – Prey utilization pattern – Prey susceptibilities – Capture success

Many animal behaviors have been studied with optimization models. In particular, optimal foraging theory has been regarded as a powerful method of predicting foraging patterns of animals. Conventional optimal foraging theory (Krebs and McCleery 1984; Stephens and Krebs 1987) emphasized that organisms should maximize a net rate of return in some currency (Schoener 1971). Using this idea, foraging models have successfully explained prey selection (Werner and Hall 1974; Krebs et al. 1977), sequence of patch use (Stephens et al. 1986), and patch departure (Krebs et al. 1974; Hodges 1985a, b). Conventional optimal foraging models of prey selection have predicted that predators should actively include certain prey types in their diets

and actively reject others (Charnov 1976). According to this theory, the inclusion of a prey type in the diet depends only on the profitability of prey types of higher ranks. Also, a certain prey type should be included in a predator's diet in an all-or-none fashion.

However, many animals do not obey this rule and show partial preferences in many cases (e.g. Greene 1986). In addition to active choice by the predators, prey selection can also be influenced by other factors that affect the relative vulnerabilities of different prey types to the predator. Difference in microhabitats inhabited by potential prey types can lead to differential encounter rates with a predator among prey types. After an encounter, differential susceptibility of the various prey types to the predator affects the success of attacks of the predator. For predators with active prey, the susceptibility of prey and probability of capture success are important factors affecting prey utilization. Conventional foraging theory has assumed that these factors are constant.

We propose that the prey utilization pattern of Ural owls (*Strix uralensis*) is only partly explained by conventional foraging theory. Contrary to the implicit assumption of optimal foraging theory, these owls appear to alter their capture success under different food conditions. In this paper we substantiate this hypothesis with observations on prey utilization by four Ural owls, paying special attention to prey susceptibility and capture success.

Materials and methods

Predator and prey species

The predator used in this study was the Ural owl (*Strix uralensis*). The Ural owl is a resident nocturnal raptor in Japan and usually uses a sit-and-wait strategy to hunt active prey. Typical prey species include the Japanese grass vole, *Microtus montebelli*, the large Japanese field mouse, *Apodemus speciosus*, and the small Japanese field mouse *A. argenteus* (Ikeda and Ishizawa 1949; Imaizumi 1968; Matsuoka 1977). Four adult owls (code named 79-A, 79-B, 84-A, and 84-B) were used. Each individual was caught as a fledgling, and reared in an aviary. When owls were not being used in the experiments, they were kept in an aviary and fed liberally on the muscular stomachs of hens.

The prey species used in this study were three species of wild mice, *M. montebelli*, *A. speciosus*, and *A. argenteus*. *M. montebelli* was mainly caught in the grassy river bed

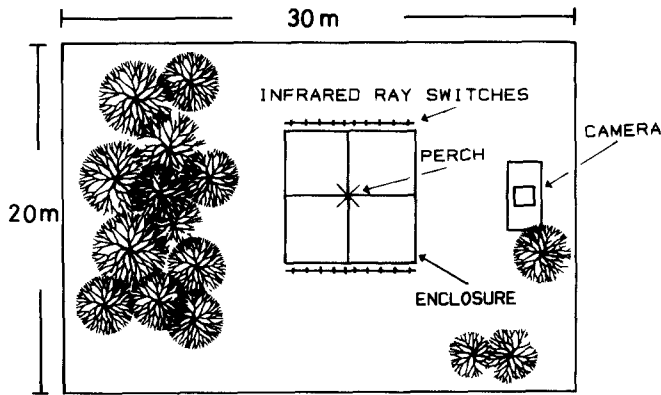


Fig. 1. A plan of the experimental cage

of the Tone River in Chiba Prefecture, Japan. *A. speciosus* was caught in pine groves around Tsukuba University. *A. argenteus* was caught at the foot of Mt. Fuji in Yamanashi Prefecture, Japan. These mice were reared in a laboratory with commercial baits.

Prey quality

The quality of each prey species was evaluated as a calorific value per individual. We sampled three *A. speciosus*, five *A. argenteus*, and nine *M. montebelli* individuals. After measuring their fresh body weights, they were dried in a vacuum for 3 days, and weighed. Each individual was ground after being frozen in liquid nitrogen. Calorific values were measured by a Nenken type adiabatic bomb calorimeter on three samples of 1 g dry weight. Calorific values were converted to calories per 1 g of fresh weight. Variation in calorific content among the three species of mice was analyzed by a nested ANOVA.

Prey utilization of owls

Owl foraging behavior was observed in a flight cage (30 × 20 × 12 m) 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 (Fig. 1). The owl roosted in this grove in day time. At the center of the cage, we set up a mouse enclosure where mice were released. The enclosure, 7.2 × 7.2 m in area and fenced with steel plate 90 cm tall, was divided into four sections. The enclosure floor was covered with soil 2 cm in depth. We set up a perch in the center of the enclosure. Wires prevented the owl from sitting on the edges of the enclosure, so the owl could detect prey in the enclosure only while on the perch.

The hunting behavior of the owl was observed on three combinations of prey species; *M. montebelli* and *A. speciosus* (Experiment I), *M. montebelli* and *A. argenteus* (Experiment II), and *A. speciosus* and *A. argenteus* (Experiment III). The three experiments were performed in a random sequence for each individual owl.

In each experiment, two mice of each species were randomly released into the four sections every night, one mouse per section. Hunting behavior was recorded with a 35 mm still camera triggered by ten pairs of infrared ray switches. When the owl cut the ray to hunt a mouse in the enclosure, the time and section of each attack were recorded automati-

cally. Next morning, the remaining mice were recaptured and the species and the numbers of mice hunted by the owl were recorded. In principle, a single experiment was conducted for 7 successive days. Unfortunately, because of insufficient film exposure, we sometimes could not obtain complete data for one night. In such cases, we conducted additional tests to make up for defective records. Since the data obtained in this study were unbalanced, we used the general linear model (GLM) procedure of SAS (SAS Institute 1982).

Results

Prey quality

The calorific values per gram fresh weight of the three species were not significantly different (Table 1). This suggests that body weight is a sufficient index of the quality of each prey species. The mean and S.E. of individual weight of prey species used in the experiments are also shown in Table 1. Because mice that survived the preceding night were released again, and body weights were measured before each release, the records of some individuals were used more than once in calculation. There was no significant difference in body weights between *M. montebelli* and *A. speciosus*, but both were significantly heavier than *A. argenteus*. Therefore, *M. montebelli* and *A. speciosus* were considered to be superior to *A. argenteus* as prey for the owls.

Attack of owls on prey mice

Prey utilization pattern of owls within experiments. Table 2 shows the numbers of each prey species captured in each experiment and the results of a heterogeneity *G*-test (Sokal and Rohlf 1981). Table 2 does not include sets in which all of the mice were taken by an owl in one night.

In experiment I, the number of each prey species taken by each owl did not show heterogeneity among owls. *M. montebelli* was captured significantly more often than *A. speciosus*. In experiment II, the heterogeneity among owls was also not significant. A significant departure from even proportions in pooled *G* indicates that *M. montebelli* was captured significantly more often than *A. argenteus*. In experiment III, the owls varied greatly in the proportions of prey species captured, but the pooled data shows that overall the number of captured individuals of each prey species was not significantly different from an even proportion. In conclusion, *M. montebelli* was caught more often than either of the two species of *Apodemus*.

Table 3 shows the proportion of capture success for each prey species. Proportion of capture success was calculated by dividing the total number of successful attacks by the total number of attacks on each prey species in each experiment. In order to know why *M. montebelli* was eaten more than the other two species, we analyzed whether the proportion of capture success was independent of prey species using a repeated *G*-test of independence (Zar 1984) (Table 3). In all experiments, there was no significant heterogeneity in the proportion of capture success for each prey species among owl individuals. The pooled data indicate that the proportion of capture success on *M. montebelli* was significantly higher than on the two *Apodemus* species, but the proportion of capture success did not differ significantly between the latter two species.

Table 1. Calorific values and weights of the three prey species (mean and SE)

	<i>Apodemus speciosus</i>		<i>A. argenteus</i>		<i>Microtus montebelli</i>		<i>F</i>	<i>P</i>
Calorific value of fresh weight (cal/g)	259.1	15.42 ^a (3)	250.2	12.56 ^a (4)	253.2	14.48 ^a (9)	0.23	0.80
Body weight (g)	32.6	1.02 ^a (92)	17.6	0.39 ^b (84)	33.0	0.65 ^a (110)	132.2	0.01

^{a,b} Values across a row with the same superscript are not significantly different at the level of $P=0.05$ (tested by GT2-test)

The number in parentheses are sample sizes

Table 2. Numbers of prey captured by individual owls. Differences analyzed by heterogeneity *G*-test

1) Experiment I								
Owl ID	Prey species		No. of nights		df	<i>G</i> value	<i>P</i> <	
	<i>Microtus montebelli</i>	<i>Apodemus speciosus</i>						
79-A	18	5	10					
84-A	7	2	5	Heterogeneity	2	0.8464	ns	
84-B	14	7	12	Pooled	1	12.2741	0.0001	
Pooled	39	14	27	Total	3	13.1205	0.005	
2) Experiment II								
Owl ID	Prey species		No. of nights		df	<i>G</i> value	<i>P</i> <	
	<i>M. montebelli</i>	<i>A. argenteus</i>						
79-A	4	2	2					
79-C	3	3	2	Heterogeneity	3	1.3778	ns	
84-A	2	1	1	Pooled	1	5.9206	0.025	
84-B	18	6	10					
Pooled	27	12	15	Total	4	7.2984	ns	
3) Experiment III								
Owl ID	Prey species		No. of nights		df	<i>G</i> value	<i>P</i> <	
	<i>A. speciosus</i>	<i>A. argenteus</i>						
79-A	3	8	11					
84-A	1	2	3	Heterogeneity	2	35.2938	0.001	
84-B	5	4	9	Pooled	1	1.0957	ns	
Pooled	9	14	23	Total	3	36.3896	0.001	

Differences in prey utilization between experiments. The average amount of prey available in one night was 136.0 g (± 3.14 g S.E., $N=24$) in experiment I, 100.5 g (± 1.92 g S.E., $N=22$) in experiment II, and 91.5 g (± 3.42 g S.E., $N=19$) in experiment III. Thus the amount of prey was largest in experiment I and smallest in experiment III. The differences in the amount of available prey between all combinations were significant ($P < 0.05$ by GT2-test).

The total numbers of attacks in one night were compared among experiments and among individual owls. No significant differences were found in either comparison (Table 4). On average, owls attacked mice about 10 times per night.

The total weight of prey acquired by owls in one night was compared among experiments and among individual owls. Weight acquired in one night was not significantly different among the three experiments nor among individ-

ual owls (Table 5). Owls took an average of 73.8 g per night over all experiments.

Table 6 shows the results of repeated *G*-tests for independence (Zar 1984) of the proportion of capture success on attack on each prey species between experiments. In all cases, there was no heterogeneity in the proportion of capture success among individual owls. The attack success rate on *M. montebelli* was significantly lower in experiment I (26%) than in experiment II (50%). Similarly the attack success rate on *A. speciosus* was significantly lower in experiment I (11%) than in experiment III (30%). However, the attack success rate on *A. argenteus* was not significantly different between experiments II and III.

Prey selection. In order to examine prey selection by owls, a null model of owl attack was developed. In this model owls attack mice randomly in proportion to the relative

Table 3. Proportion of capture success in each experiment and repeated *G*-test of independence between capture success and prey type

1) Experiment I						
Owl ID	Prey species			df	<i>G</i> value	<i>P</i> <
	<i>Microtus montebelli</i>	<i>Apodemus speciosus</i>				
79-A	11/33 (33%)	6/47 (13%)	Heterogeneity Pooled	2	0.0720	ns
84-A	7/40 (18%)	2/27 (7%)		1	6.3999	0.025
84-B	3/17 (18%)	1/ 8 (13%)				
Pooled	21/80 (26%)	9/82 (11%)	Total	3	6.4719	0.025

2) Experiment II						
Owl ID	Prey species			df	<i>G</i> value	<i>P</i> <
	<i>M. montebelli</i>	<i>A. argenteus</i>				
79-A	8/19 (42%)	6/16 (38%)	Heterogeneity Pooled	3	7.4789	ns
79-B	3/ 6 (50%)	3/18 (17%)		1	10.7075	0.005
84-A	6/14 (43%)	5/19 (26%)				
84-B	8/11 (73%)	1/17 (6%)				
Pooled	25/50 (50%)	15/70 (21%)	Total	4	18.1864	0.005

3) Experiment III						
Owl ID	Prey species			df	<i>G</i> value	<i>P</i> <
	<i>A. speciosus</i>	<i>A. argenteus</i>				
79-A	5/24 (21%)	7/29 (24%)	Heterogeneity Pooled	2	1.4260	ns
84-A	9/24 (38%)	10/26 (38%)		1	0.0787	ns
84-B	7/22 (32%)	7/34 (21%)				
Pooled	21/70 (30%)	24/89 (27%)	Total	3	1.5047	ns

Numerators and denominators are success numbers and attack numbers respectively

Table 4. The number of attacks per night in experiments I, II, and III, and the result of a two-way ANOVA

Owl ID	Experiment								
	I			II			III		
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>
79-A	13.0	3.29	6	8.8	2.00	4	13.6	3.20	4
79-B	—	—	—	12.0	9.87	2	—	—	—
84-A	11.4	4.34	5	11.0	2.00	3	10.2	3.90	5
84-B	8.3	2.52	3	7.0	3.46	4	9.3	3.33	6
Total	11.4	3.78	14	9.2	4.09	13	10.7	3.64	15

Source of variation	df	MS	<i>F</i>	<i>P</i> <
Experiments	2	16.4017	1.16	0.3250
Owls	3	33.9425	2.14	0.0853
Interaction	4	8.5478	0.61	0.6607
Error	32	14.0885		

Table 5. Total prey weight taken by an owl per night (g) in experiments I, II, and III, and the result of a two-way ANOVA

No. of owl	Experiment								
	I			II			III		
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>
79-A	91.1	33.18	12	87.2	14.96	5	69.5	22.39	6
79-B	—	—	—	74.0	7.07	2	—	—	—
84-A	63.8	33.94	5	93.3	21.78	3	79.6	13.61	5
84-B	68.6	41.20	14	72.1	17.08	12	49.3	22.31	8
Total	75.7	38.71	31	78.6	17.89	22	63.7	23.97	19

Source of variation	df	MS	<i>F</i>	<i>P</i> <
Experiments	2	1341.6718	1.66	0.1990
Owls	3	2122.9643	2.61	0.0585
Interaction	4	749.6511	0.93	0.4548
Error	62	809.6388		

Table 6. The tests of proportion of capture success on each prey species between experiments

Test	df	G value	P <
1) Comparison of attacks on <i>Microtus montebelli</i> between experiments I and II			
Pooled	1	6.9640	0.025
Heterogeneity	2	3.9139	ns
Total	3	10.8779	0.01
2) Comparison of attacks on <i>Apodemus speciosus</i> between experiments I and III			
Pooled	1	8.7409	0.005
Heterogeneity	2	0.4345	ns
Total	3	9.1754	0.05
3) Comparison of attacks on <i>A. argenteus</i> between experiments II and III			
Pooled	1	0.2637	ns
Heterogeneity	2	3.4856	ns
Total	3	3.7493	ns

representation of prey species among the remaining prey individuals. Within an experiment the probability of an attack ending in a successful capture is assumed to depend only on the prey species. This prey-species-specific capture probability was estimated as the proportion of all attacks on each prey species during the experiment which were suc-

cessful. Under this model the probability of attacking a prey species changes after each successful capture because the relative prey species proportions change. After a few attacks the calculation of these probabilities becomes quite complex. Formally it is easiest to consider this model as a Markov process. The details of the state-space and the transition matrix are developed in the appendix.

Using this technique the expected number of attacks on each prey species under the null model can be calculated for each experiment. For example in experiment I, with a *M. montebelli* capture success of 0.26 and a *A. speciosus* capture success of 0.11 (see Table 3), if an owl attacks 9 times in a night, the expected number of attacks on *M. montebelli* is 3.98 and that on *A. speciosus* is 5.02. Table 7 lists the observed and expected number of attacks on the three prey species for available data in all experiments. In only 5 out of 42 nights did the observed number of attacks deviate significantly from the expected (*G*-test, $p < 0.05$). However, because the number of attacks each night was so small, we have a high risk of type II error when testing goodness of fit for a single night. So, using the additivity of *G*-values, we further tested total *G*-value with degrees of freedom equal to the number of nights available to each individual owl and to all owls for each experiment. Significant differences in the attack frequency on each prey species were not observed in any experiment. These results show that the number of attacks on two prey species in one night did not deviate significantly from the proposed null model.

In order to analyze the attack pattern of owls in more detail, the probabilities with which all possible sequences of the first five attacks would occur under the random at-

Table 7. Comparison between observed and hypothetical relative frequencies of attacks to each prey species. Each row shows cumulative attacks in each night. See text for further details

Owl ID	Observed no. attacks		Predicted no. attacks		G value	df	P <
	<i>Microtus montebelli</i>	<i>Apodemus speciosus</i>	<i>M. montebelli</i>	<i>A. speciosus</i>			
a) Experiment I							
79-A	3	6	3.98	5.02	0.444	1	ns
	7	9	6.21	9.79	0.162	1	ns
	6	8	5.65	8.35	0.036	1	ns
	7	2	3.98	5.02	4.224	1	0.05
	5	12	6.47	10.53	0.559	1	ns
	5	10	5.94	9.06	0.252	1	ns
Total					5.677	6	ns
84-A	6	6	5.03	6.97	0.318	1	ns
	5	3	3.60	4.40	0.987	1	ns
	10	5	5.94	9.06	4.473	1	0.05
	4	2	2.79	3.21	0.990	1	ns
	5	11	6.21	9.79	0.397	1	ns
Total					7.165	5	ns
84-B	5	3	3.60	4.40	0.987	1	ns
	8	3	4.70	6.30	4.058	1	0.05
	4	2	2.79	3.21	0.990	1	ns
Total					6.035	3	ns
Grand total					18.877	14	ns

Table 7 (continued)

b) Experiment II

Owl ID	Observed no. attacks		Predicted no. attacks		G value	df	P <
	<i>M. montebelli</i>	<i>A. argenteus</i>	<i>M. montebelli</i>	<i>A. argenteus</i>			
79-A	7	3	3.70	6.30	4.474	1	0.05
	4	6	3.70	6.30	0.038	1	ns
	5	4	3.46	5.54	1.076	1	ns
	3	3	2.59	3.41	0.113	1	ns
Total				5.701	4	ns	
79-C	5	14	4.88	14.12	0.004	1	ns
	1	4	2.23	2.77	1.336	1	ns
Total				1.340	2	ns	
84-A	5	8	4.25	8.75	0.191	1	ns
	5	4	3.46	5.54	1.076	1	ns
	4	7	3.91	7.09	0.003	1	ns
Total				1.270	3	ns	
84-B	3	2	2.23	2.76	0.491	1	ns
	3	1	1.85	2.15	1.370	1	ns
	2	5	2.91	4.09	0.509	1	ns
	3	9	4.09	7.91	0.464	1	ns
Total				2.834	4	ns	
Grand total				11.145	13	ns	

c) Experiment III

Owl ID	Observed no. attacks		Predicted no. attacks		G value	df	P <
	<i>A. argenteus</i>	<i>A. speciosus</i>	<i>A. argenteus</i>	<i>A. speciosus</i>			
79-A	6	6	5.85	6.15	0.008	1	ns
	8	10	8.64	9.36	0.091	1	ns
	6	5	5.38	5.62	0.140	1	ns
	9	3	5.85	6.15	3.447	1	ns
Total				3.686	4	ns	
84-A	6	3	4.42	4.58	1.129	1	ns
	3	5	3.94	4.06	0.447	1	ns
	6	9	7.26	7.74	0.427	1	ns
	8	5	6.32	6.68	0.875	1	ns
	3	2	2.48	2.52	0.218	1	ns
Total				3.096	5	ns	
84-B	2	3	2.48	2.52	0.186	1	ns
	9	6	7.26	7.74	0.811	1	ns
	5	5	4.90	5.10	0.004	1	ns
	8	2	4.90	5.10	4.099	1	0.05
	5	3	3.94	4.06	0.567	1	ns
	5	3	3.94	4.06	0.567	1	ns
Total				6.234	6	ns	
Grand total				13.016	15	ns	

tack model were calculated explicitly. The first five attack sequences were observed 14, 13, and 15 times in experiments I, II, and III, respectively. Probabilities for these sets of sequences were estimated by Monte Carlo simulation. Twenty thousand sets of 14, 13, and 15 five-attack sequences were randomly generated. The probability of each set of sequences was estimated for each experiment. By 20000 samples the calculated proportions were quite stable to change in sample size. We calculated the number of randomly chosen sets of sequences which had a probability of occurrence less than the probability of occurrence of the observed set. The proportions thus generated was used as a type I error level. The error levels were 0.858, 0.833, and 0.916 in experiments I, II, and III respectively. So this result also supports the hypotheses that owls attack at random and that capture success depends on the escape ability of the prey.

Discussion

Throughout the study, owls attacked mice about 10 times a night. *Microtus montebelli* were taken more than either *Apodemus* species. The number of attacks on each prey species was close to the proportion predicted by the random attack model. However the proportion of capture success differed among prey species, i.e. it was higher for *M. montebelli* than for *A. speciosus* and *A. argenteus*. This means that *M. montebelli* was more susceptible to attack by owls than the two *Apodemus* species. These results indicate that owls attacked mice without discriminating between prey types, and that the differences in the number of mice of each species captured was mostly due to differences in susceptibility among prey species.

A conventional prey selection model (as summarized by Stephens and Krebs 1987, 17–24) can predict the behavior of foragers which discriminate between prey types and actively choose certain types of prey. The model can also be used for the case in which even such foragers may forage indiscriminately. We utilized a prey choice model for the foraging of owls in which one parameter is added to the conventional ones. Suppose that there are two prey types. Four parameters characterize each prey type:

- E_i = energy derived from prey i ,
- P_i = susceptibility of prey i
(probability of capture success of prey i),
- λ_i = encounter rate of prey i ,
- h_i = handling time of prey i .

In conventional theory P_i has been implicitly considered to be unity, but in our case P_i is an adjustable parameter. If prey type 1 is more profitable than prey type 2 (i.e., $E_1 * P_1 / h_1 > E_2 * P_2 / h_2$), foragers encounter prey types at random, and the following inequality is satisfied,

$$1/\lambda_1 > (E_1 * P_1 * h_2) / (E_2 * P_2) - h_1 \quad (1)$$

(modified from an inequality in Stephens and Krebs 1987, p. 19) the forager attacks not only the more profitable prey type but also the less profitable one. In other words, foragers attack prey indiscriminately. How many prey of each species a forager captures depends on encounter rate (λ_i) and probability of capture success (P_i). In this study, the ratio of energy derived from the three prey species was *M. montebelli*: *A. speciosus*: *A. argenteus* = 2:2:1 (Table 1).

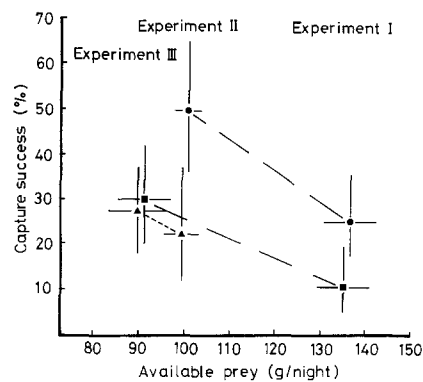


Fig. 2. Attack success rate on each prey species in three experiments. ● = *Microtus montebelli*, ■ = *Apodemus speciosus*, and ▲ = *A. argenteus*. Vertical and horizontal bars represent 95% confidence limits. A dashed line connecting experiments indicates a significant difference in attack success rates on the indicated prey species, while a dotted line indicates a lack of significance at $P < 0.05$.

Handling time was 1–2 s (unpublished data), and did not differ among the three prey species. Owls attacked 10 times a night, so waiting time, $(1/\lambda_i)$, was much longer than handling time. Thus the conditions leading to indiscriminate attack were satisfied in all experiments of this study. Conventional foraging theory may well explain the random attack pattern of the owls. However, the variation in capture success between prey species was much larger than that in encounter rate. So capture success might contribute more than encounter rate to the variation in numbers of prey captured between prey species.

Therefore, both indiscriminate foraging behavior and conventional foraging theory for discriminative foragers could explain the observed random pattern of attacks of owls. Although owls use auditory cues to recognize the presence of prey in the dark (Konishi 1973), these cues may not be sufficient to discriminate among prey types. If this is true, indiscriminate foraging may be a more reasonable explanation for the random attack by owls. In both models, conventional foraging theory and lack of discrimination of prey, prey susceptibility was the most important factor affecting prey utilization. Thus it is unlikely that active selection of prey type affected prey utilization patterns.

The mean rewards for owls per night did not differ significantly among experiments with different food conditions. Energy intake per night is determined by encounter rate, capture success, and prey size. Encounter rates in all experiments were almost equal, about 10 times a night. Thus energy intake was affected by capture success under different food conditions. Proportion of capture success for each prey species varied with food conditions. The proportion of capture success for all prey species was higher in experiments with less profitable prey conditions than in those with more profitable ones (Fig. 2). Since it is unlikely that the mice changed their escape ability between experiments, the differences in capture success are most probably due to changes in owl behavior.

According to conventional optimal foraging theory, animals should behave so as to maximize some currency of fitness such as energy intake rate (net energy gain/unit time) (Schoener 1971), or energy efficiency (net energy gain/unit energy expenditure) (Schmid-Hempel et al. 1985). In order

to maximize these criteria, in many cases, the predicted behavior of animals should have no variation and is decided by a simple rule.

Conventional optimal foraging theory implicitly assumes that the foragers' probability of capture success does not change under any food conditions. Theory predicts that if cost (number of attacks) is constant, energy gain is greater in more profitable food conditions, and that if energy gain is constant, cost is more in less profitable conditions. Our results do not conform to these predictions. Energy gain was approximately constant for all experiments because the proportion of capture success changed with food condition. Therefore, the assumptions of conventional optimal foraging theory cannot apply to the hunting behavior of owls. Even though in our case, changes in the proportion of capture success were not reflected in the prey selection pattern, changing the probability of capture success for a predator with active prey may influence the prey utilization pattern.

There are two approaches to explain the owls' capture success for the same prey type changed. First, we could try to find further constraints that restrict animal behavior in a optimal foraging model, such as predation risk (Milinski and Heller 1978), territorial defense (Ydenberg and Houston 1986), complementary nutrient constraints (Belovsky 1978), recognition ability (Getty and Krebs 1985), discounting of future rewards (Kagel et al. 1986), variability of time estimation ability (Houston and McNamara 1985), and so on. Still, these constraints may not be able to explain the variations of capture success with food condition in this study. Second, we could challenge the underlying hypothesis of conventional optimal foraging models. In conventional models, the currency mentioned above has an assumed linear relationship with fitness. It is unlikely however that a real animal's fitness will have a linear relationship with any currency even if other factors are assumed to be constant (Caraco 1980; Real 1980a, b). McNamara and Houston (1982, 1986) also demonstrated non-linear relationships between energy reserve and fitness in their simulation models. If we suppose that the fitness function to energy gain of owls per night is S-shaped as McNamara and Houston (1986) suggested, increasing gain and increasing number of attacks may result in little increase and decrease of fitness respectively when an owl has a chance to take adequate prey to satisfy its energy need for one night and the energy expenditure of an attack is small compared with the total energy gain per night. We believe that this is the case in the present experiments. Sih (1982) arrived at similar conclusions in his empirical study on changing feeding rate in the backswimmer, *Notonecta hoffmanni*. Thus for owls in this study the reduced capture success in profitable prey conditions may cause little decline of fitness. On the other hand, intense concentration on an attack, while resulting in high capture success, may be stressful to individual owls. If so, decreasing capture success may be useful to reduce stress to individuals while still keeping fitness high under a condition with sufficient prey. In this case, prior experiences of gain per successful attack could also influence the capture success.

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Appendix

There are nine possible states of prey availability. These states are indexed as follows; 1. (2,2), 2. (1,2), 3. (2,1), 4. (0,2), 5. (1,1), 6. (2,0), 7. (0,1), 8. (1,0), 9. (0,0); where the numbers in parentheses represent the number of individuals of each prey species available in the given state. We show an example of the calculations for experiment I. We estimate the owl's probability of capture success for each prey species, m for *M. montebelli* and s for *A. speciosus*, by dividing the number of successful attacks on each prey species by the total number of attacks on that prey species. The state transition matrix is then given by

$$M = \begin{bmatrix} 1-(m+s)/2 & s/2 & m/2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1-(s+2m)/3 & 0 & s/3 & 2m/3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1-(2s+m)/3 & 0 & 2s/3 & m/3 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-m & 0 & 0 & m & 0 & 0 \\ 0 & 0 & 0 & 0 & 1-(m+s)/2 & 0 & s/2 & m/2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1-s & 0 & s & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1-m & 0 & m \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1-s & s \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Each element m_{ij} in matrix M shows the transition probability from state i to state j . The probability distribution vector after the t -th attack is \mathbf{b}_t . The initial probability distribution is

$$\mathbf{b}_0 = (1, 0, 0, 0, 0, 0, 0, 0, 0)$$

(i.e. the probability is 1 that the system is in state 1). Because probability of attack on each prey species is equal to the proportion of each prey species surviving, attack probabilities are given by the constant vectors

$$\mathbf{c}_m = (1/2, 1/3, 2/3, 0, 1/2, 1, 0, 1, 0) \text{ on } M. \text{ montebelli}$$

and

$$\mathbf{c}_s = (1/2, 2/3, 1/3, 1, 1/2, 0, 1, 0, 0) \text{ on } A. \text{ speciosus}$$

in each state. Here, $c_j(i)$ is the probability that the owl will attack prey species j when the system is in state i . The probability distribution vector after t -th attack is expressed as follows

$$\mathbf{b}_t = \mathbf{b}_{t-1} * M = \mathbf{b}_0 * M^t.$$

Given that there is a t -th attack, the probability that the t -th attack is on *M. montebelli*, P_{mt} , is given by

$$P_{mt} = \frac{\mathbf{c}_m \cdot \mathbf{b}'_t}{\mathbf{c}_m \cdot \mathbf{b}'_t + \mathbf{c}_s \cdot \mathbf{b}'_t}.$$

Similarly, the conditional probability that the t -th attack is on *A. speciosus* is given by

$$P_{st} = \frac{\mathbf{c}_s \cdot \mathbf{b}'_t}{\mathbf{c}_m \cdot \mathbf{b}'_t + \mathbf{c}_s \cdot \mathbf{b}'_t}.$$

Where \mathbf{b}'_t is the transpose of \mathbf{b}_t , $\mathbf{c}_m \cdot \mathbf{b}'_t$ and $\mathbf{c}_s \cdot \mathbf{b}'_t$ are the inner products of the attack probability vector with the probability distribution vector, and P_{ij} is the probability of attack on prey species i at j -th attack, given that the j -th attack occurs. Therefore the expected total number of attacks on *M. montebelli* and *A. speciosus* by the end of the T -th attack are

$$\sum_{t=0}^T P_{mt}$$

and

$$\sum_{t=0}^T P_{st} \text{ respectively.}$$

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