FACTORS INFLUENCING PREY SELECTION IN THE AMERICAN KESTREL[1]

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PIELOWSKI (1959, 1961) showed that Goshawks (*Accipiter gentilis*) prefer as prey domestic pigeons (*Columba livia*) that differ in color from the majority of the population. He systematically picked up the remains of Goshawk kills in a Poland forest and found that domestic pigeons were an important prey item and that 60% of the pigeons taken were dark colored. A survey of the pigeon lofts in the nearby villages revealed that the population contained only 13% dark birds. Pielowski then established a pigeon loft and stocked it with 86% dark colored birds and 14% birds with considerable white in the plumage. In this situation 35% of the attacks were directed at largely white birds. The Goshawks thus seemed to prefer odd, or unusually colored pigeons. Salt (1967) showed how these and other data fit rather well into the generalization that predators prefer odd animals. As odd pigeons are relatively conspicuous among the birds with which they are flying, Pielowski's Goshawks possibly were merely selecting pigeons on the basis of their conspicuousness. The selection of conspicuous prey has been demonstrated for a variety of vertebrate predators (e.g. Sumner 1935, Isely 1938, Dice 1947).

In the past several years I have attempted to determine the factors influencing prey selection in American Kestrels (*Falco sparverius*) by conducting controlled experiments in the laboratory with gray and white laboratory mice as prey. In my first experiments (Mueller 1968) I found that conspicuousness appeared important, but the results were difficult to interpret because my hawks showed a tendency to continue selecting a given color of mouse, largely regardless of other variables. Tinbergen (1960) found that tits (Paridae) tend to select one kind of larval Lepidoptera at any given time and believed that the birds were actively searching for these specific larvae and largely ignoring other potential prey. Tinbergen labeled this phenomenon a "specific searching image" (SSI). My second series of experiments (Mueller 1971) indicated that an SSI was the most important determinant of prey selection but that oddity appeared to be nearly as important. I designed the experiments reported in the present paper to delineate the influence of the SSI in prey selection and explore the mechanism by which it is formed.

TABLE 1

EXPERIMENTAL DESIGN FOR EACH SERIES

	No. of experiments	Mice presented in each experiment		Expected catch[1]	
		SSI color	Other color	SSI color	Other color
Train	30	10	0	30	0
Test 1	50	9	1	45	5
Test 2	25	8	2	20	5
Test 3	18	7	3	12.6	5.4
Test 4	13	6	4	7.8	5.2
Test 5	10	5	5	5	5
Test 6	13	4	6	5.2	7.8
Test 7	18	3	7	5.4	12.6
Test 8	25	2	8	5	20
Test 9	50	1	9	5	45

[1] Assuming random selection.

METHODS AND MATERIALS

Five American Kestrels were used in the experiments, three males and two females. One of the males (Frodo) was taken as a 3-week old nestling and hand-reared in my laboratory; the other four birds were trapped in fall or winter with a bal-chatri (Mueller and Berger 1959). Gandalf and Frodo had been used in previous experiments; the remaining three birds were trapped shortly before the experiments began. The birds were tamed and acclimated to the laboratory and the experimenters and then accustomed to capturing live mice in the test environment.

Albino laboratory mice, some of which were dyed gray with a tasteless food dye, were used as prey. In each experiment 10 mice were presented, each mouse on a pedestal 10-cm square and 15-cm high. Laboratory mice rarely leave such a pedestal, so the spatial distribution of mice can be controlled. The pedestals were arranged 10 cm apart on an arc 1.9 m long of a circle of 2 m radius (12.6 m circumference). The hawk was placed on a perch at the center of the circle and 85 cm above the level of the pedestals. The pedestals and the entire substrate behind the mouse in view of the kestrel were painted either white or gray to match one of the colors of mice. Measurement of four photographs taken with the camera at the kestrel's perch revealed that, on the average, the 10 mice covered 1.6% of the background. The mean distance between mice was 2.9 times their average apparent width. The positions of the two colors of mice in the arc array were randomized.

TABLE 2

EXPERIMENTAL DESIGN: DIFFERENCES BETWEEN SERIES

Experiment series	SSI[1] color	Substrate color	Other attributes of SSI[1] mice	
			Tests 1–5	Tests 6–9
A	White	Gray	Conspicuous	Odd, Conspicuous
B	Gray	Gray		Odd
C	Gray	White	Conspicuous	Odd, Conspicuous
D	White	White		Odd

[1] Short-term specific searching image.

TABLE 3

RESULTS OF EXPERIMENTS, SERIES A[1]

	Expected value	Gandalf	Frodo	Aragorn	Gala	Varda
Test 1	0.90	0.94	0.88	0.58 −	0.78 −	0.92
Test 2	0.80	1.00 +	0.88	0.55 −	0.80	1.00 +
Test 3	0.70	0.94 +	0.94 +	0.44 −	0.78	1.00 +
Test 4	0.60	1.00 +	0.54	0.38	0.77	1.00 +
Test 5	0.50	1.00 +	0.50	0.10 −	1.00 +	1.00 +
Test 6	0.40	1.00 +	0.69	0.31	0.92 +	0.92 +
Test 7	0.30	1.00 +	0.67 +	0.39	0.72 +	1.00 +
Test 8	0.20	0.92 +	0.64 +	0.16	0.96 +	1.00 +
Test 9	0.10	1.00 +	0.54 +	0.10	0.82 +	1.00 +
TOTAL	0.50	0.97 +	0.72 +	0.33 −	0.83 +	0.98 +

[1] Substrate gray, SSI white. The results are expressed as the number of SSI mice taken divided by the number of experiments and thus as the proportion of SSI mice taken. + indicates that significantly more SSI mice were taken than predicted by random selection, − fewer ($p < 0.05$, Chi-square test).

The experimental design used with each kestrel is presented in Tables 1 and 2. Basically, each kestrel was presented with no choice of color of mice for 30 trials, on the assumption that it would establish an SSI for that color. The bird was then offered nine mice of the the SSI color and one mouse of the other color for 50 experiments (test 1), then eight mice of the SSI color and two of the other color for 25 experiments (test 2), and so on until it was finally offered one mouse of the SSI color and nine of the other color (test 9). The kestrel was allowed to capture only one mouse in each experiment. The number of trials in each test was set so that the minimum expected value (assuming random selection) was five or more for either color of mouse (Table 1). This sequence of tests was performed four times with each kestrel, beginning each time with a different combination of mouse and substrate color (series A, B, C, D, Table 2). The experimental design is symmetrical, with conspicuousness, oddity, and the SSI color occurring in various combinations. Each of the five kestrels thus performed 888 selections in the course of the study.

No statistical test is completely appropriate for my experimental design because the data for each of my experimental tests are a series of repeated measures and all

TABLE 4

RESULTS OF EXPERIMENTS, SERIES B[1]

	Expected value	Gandalf	Frodo	Aragorn	Gala	Varda
Test 1	0.90	0.60 −	0.66 −	0.88	0.46 −	0.12 −
Test 2	0.80	0.76	0.80	0.68	0.20 −	0 −
Test 3	0.70	0.94 +	0.78	0.44 −	0.05 −	0 −
Test 4	0.60	0.85	0.85	0.08 −	0.15 −	0 −
Test 5	0.50	1.00 +	0.60	0.10 −	0.20	0 −
Test 6	0.40	0.54	0.77 +	0.15	0.08 −	0 −
Test 7	0.30	0.67 +	0.67 +	0.17	0.06 −	0 −
Test 8	0.20	0.80 +	0.60 +	0.20	0.04 −	0 −
Test 9	0.10	0.28 +	0.40 +	0.12	0.02	0.02
TOTAL	0.50	0.63 +	0.64 +	0.39 −	0.17 −	0.03 −

[1] Substrate gray, SSI gray. See Table 3 for explanation.

TABLE 5

RESULTS OF EXPERIMENTS, SERIES C[1]

	Expected value	Gandalf	Frodo	Aragorn	Gala	Varda
Test 1	0.90	0.56 −	0.98	0.34 −	0.32 −	0.88
Test 2	0.80	0.32 −	0.88	0.16 −	0.32 −	0.28 −
Test 3	0.70	0.33 −	1.00 +	0.06 −	0.44 −	0.17 −
Test 4	0.60	0.08	1.00 +	0.15 −	0.38	0.08 −
Test 5	0.50	0.90 +	0.90 +	0.10 −	0.60	0.30
Test 6	0.40	0.62	1.00 +	0 −	0.38	0.77 +
Test 7	0.30	1.00 +	0.94 +	0.06 −	0.22	0.39
Test 8	0.20	0.60 +	0.76 +	0.08	0.12	0.12
Test 9	0.10	0.40 +	0.74 +	0.04	0.02	0.02
TOTAL	0.50	0.51	0.89 +	0.14 −	0.25 −	0.36 −

[1] Substrate white, SSI gray. See Table 3 for explanation.

tests are related samples. After considerable consultation with several statisticians, I chose an analysis of variance (split-plots-in-time, Steel and Torrie, 1960) as most nearly appropriate for this type of experiment. The Chi-square test has been used on very similar experimental data by many workers and I have used it to indicate the possible significance of each datum in Tables 3 through 8. The reader is urged to view all statements of significance with caution as the data may not meet the assumptions on which the statistical tests are based.

RESULTS AND INTERPRETATION

The selections made by each of the five birds are shown in Tables 3 through 6. The results are expressed as the number of mice of the SSI color taken, divided by the number of trials. This number thus states the ratio of SSI mice taken or, if the decimal is dropped, the percentage taken. A plus indicates that more mice of the SSI color (white for Table 3) were taken than expected on the assumption of random selection, and a minus indicates that fewer mice of the SSI

TABLE 6

RESULTS OF EXPERIMENTS, SERIES D[1]

	Expected value	Gandalf	Frodo	Aragorn	Gala	Varda
Test 1	0.90	0.12 −	0.82	1.00 +	0.98	0.96
Test 2	0.80	0.68	0.52 −	0.96 +	1.00 +	1.00 +
Test 3	0.70	0.39 −	0.89	0.94 +	0.83	0.89
Test 4	0.60	0.77	0.54	1.00 +	1.00 +	0.54
Test 5	0.50	0.60	0.40	0.90 +	1.00 +	0.60
Test 6	0.40	0.77 +	0.31	0.85 +	0.92 +	0.31
Test 7	0.30	0.78 +	0.17	0.83 +	0.89 +	0.56 +
Test 8	0.20	0.52 +	0.20	0.92 +	0.52 +	0.52 +
Test 9	0.10	0.30 +	0.06	0.78 +	0.14	0.26 +
TOTAL	0.50	0.44	0.43 −	0.91 +	0.72 +	0.64 +

[1] Substrate white, SSI white. See Table 3 for explanation.

TABLE 7
SUMMARY OF INDIVIDUAL PREFERENCE[1]

	Bird				
	Gandalf	Frodo	Aragorn	Gala	Varda
SSI	A	C	D		A
Conspicu-ousness	A	C		B	A, B
Oddity	B, C, D	B		A	
Color	A	C	C, D	B, D	A, B
Color preference[2]	W-G	W-G	G-W	W	W
Percent	57 (W)	59 (G)	68 (W)	78	81

[1] The letters indicate the experimental series in which the birds showed a consistent preference for the short-term SSI, conspicuousness, or a given color of mouse. Also indicated is any preference for oddity.

[2] The overall color preference (white or gray) of each hawk is given in the last two lines, along with the percent of that color taken. (Three birds shifted preferences.)

color were taken than expected (and therefore, in Table 3, that more gray mice were taken than expected). In Table 3, a plus also indicates a selection for conspicuous mice as SSI mice were white and the substrate was gray (cf. Table 2). A selection for odd mice is indicated by a negative sign in tests 1 through 4 (gray mice selected) and a positive sign in tests 6 through 9 (white mice selected). Thus, in series A, Gandalf and Varda showed a distinct tendency to select mice of the SSI color (and thus conspicuous, white mice); Frodo and Aragorn a weak, but similar, tendency; and Gala showed at least somewhat of a tendency to select odd mice.

A comparison of Table 7 and the appropriate table for each series of experiments (A, B, C, D, Tables 3 through 6) will help the reader comprehend the inter- and intraindividual variation in prey selection. Four birds showed a definite, consistent preference for the SSI color but each in only one experimental series. It is interesting to note that in one of the four cases (Gala) this preference for the SSI was also for inconspicuous mice. All four cases also could be interpreted as selection for a preferred color of mice throughout most of the experiments, which raises the question as to whether these apparent cases of selection for the SSI were artifacts resulting from an overall preference for a certain color. Four birds showed a definite overall preference for white mice ranging from 57 to 81% of the mice taken, and one bird showed a preference for gray mice (Table 7). As the experimental design is symmetrical with regard to SSI and conspicuousness, we would expect the hawks to show no overall preference for a given color of mouse. Yet consistent selection of mice of a given color occurred in 8 individual series (out of a possible 20) as compared with 4 or 5 for the other factors influencing prey selection. All cases of selection

TABLE 8

RESULTS: POOLED DATA FOR ALL FIVE HAWKS[1]

	Expected value	Series				
		A	B	C	D	Total
Test 1	0.90	0.82 −	0.54 −	0.62 −	0.78 −	0.69 −
Test 2	0.80	0.82	0.49 −	0.39 −	0.83	0.63 −
Test 3	0.70	0.83 +	0.44 −	0.40	0.79	0.62 −
Test 4	0.60	0.74 +	0.38 −	0.34 −	0.77 +	0.56
Test 5	0.50	0.72 +	0.38	0.56	0.70 +	0.59 +
Test 6	0.40	0.77 +	0.31	0.55 +	0.63 +	0.57 +
Test 7	0.30	0.76 +	0.31	0.52 +	0.64 +	0.56 +
Test 8	0.20	0.74 +	0.33 +	0.34 +	0.54 +	0.48 +
Test 9	0.10	0.69 +	0.17 +	0.24 +	0.31 +	0.35 +
TOTAL	0.50	0.77 +	0.37 −	0.43 −	0.63 +	0.55 +

[1] See Table 3 for explanation.

for conspicuous mice also can be interpreted as an overall color prefer-
ence, which raises the question of what factor is the most important.

    This overall color preference is of further interest because the birds
did not exhibit it with equal intensity through all four series. Indeed,
three of the five birds appeared to switch color preferences in series B.
Gandalf showed a very high preference for white mice in series A but
then took more gray than white mice in series B, C, and D; his over-
all preference for a color, with the switch taken into account, was
64%. Frodo took more white than gray mice in series A, but then took
more gray than white mice in series B, C, and D; his overall preference
for a color, with the switch, was 67%. Aragorn took more gray than
white mice in series A, but then switched to a consistent preference
for white mice in series B, C, and D, and showed an overall color pref-
erence of 81%. The remaining two birds, Gala and Varda, took more
white than gray mice in all four series, although the intensity and con-
sistency of the preference varied from series to series. This overall
color preference can be regarded as a long-term SSI, one that appears
to be largely unaffected by my experimental efforts to establish and
switch SSI's, and one that I cannot explain satisfactorily. The estab-
lishment of a long-term SSI for white in two of the wild-caught birds
(Gala, Varda) and gray in the other (Aragorn) is inexplicable, as is
Aragorn's switch to white in series B. Gandalf and Frodo had been
used in previous experiments (Mueller 1971), in which Gandalf had
shown a very strong preference for white mice and Frodo a moderate
preference for white mice. Both birds retained this preference through
series A but then inexplicably switched to gray in series B. In the
remainder of the paper I shall use long-term SSI to apply to prolonged
color preferences in the birds and short-term SSI to denote the prefer-

ence expected on the basis of the 30 trials without choice of color of mouse that preceded each series (A, B, C, D, Tables 1, 2).

The six cases of selection for oddity, however slight, are of extreme interest as selection for odd or uncommon mice does not coincide with concurrent selection for other factors. Evidence of selection for oddity is produced when a hawk selects mice that are not of the short-term SSI color in tests 1 through 4 and then switches to the short-term SSI color for tests 6 through 9. Under these circumstances conspicuousness can be ruled out because, regardless of substrate color, odd mice will be conspicuous only at either the first half or last half of the sequence of tests.

The significance of the results and the interactions between the four factors influencing selection are difficult to comprehend by viewing Tables 3 through 7. Table 8 presents the pooled data for all five hawks, which permits easier comprehension of the overall picture but also obscures some important intra- and interindividual differences. Further insight into the significance of the results might be gained from the analysis of variance, which tested five sources of variation: between birds, between series, between tests (which can comment on the influence of oddity), and the effects of conspicuousness and the short-term SSI. Of these, only the between birds variance is less than the residual variance and is not involved in higher order interactions. Two main effects are statistically significant, the between tests and the short-term SSI (both $P < 0.005$), but both are involved in higher order interactions that must be examined before we attach significance to the main effects. Two first-order interactions are statistically significant: tests $\times$ series ($P < 0.005$) and tests $\times$ conspicuousness ($P < 0.01$). One second-order interaction is statistically significant: tests $\times$ short-term SSI $\times$ conspicuousness ($P < 0.005$).

Unfortunately I did not anticipate a long-term SSI, and neither the experimental design nor the analysis of variance take this factor into account. Yet it is the long-term SSI that appears to influence all other sources of variance. For example, conspicuousness is involved in two interactions, but if we take the long-term SSI into account we find little or no evidence for the selection of conspicuous mice. The greatest total of conspicuous mice taken was 295 in series A, of which Varda and Gala captured 179. Series D differs from series A only in color of substrate, and hence, conspicuousness of mice (Table 2) and in series D 142 more cryptic mice were taken than expected. Varda and Gala captured 80 cryptic mice in series D. Thus Varda and Gala captured 99 more white mice in series A where these were conspicuous, than in series D where they were cryptic, but only in series A did the birds select conspicuous mice. Aragorn captured 37 more cryptic mice in

series A than expected, and 90 more cryptic mice than expected in series D because he switched his overall color preference from gray to white between series A and B. Similarly Gandalf and Frodo switched their overall preferences between series A and B and thus showed a selection for conspicuous mice in series A and a selection of cryptic mice in series D. A comparison of series B and C yields fewer inconsistencies and better evidence for the selection of conspicuous mice. But even here Gandalf took more gray mice when they were cryptic (series B) than when they were conspicuous (series C), and Aragorn took more white mice when they were cryptic (series C) than when they were conspicuous (series B).

The difference between series and the tests × series interaction also appears to be an artifact of the long-term SSI. In this case the major cause of the variance is the switch in preference of three birds (Gandalf, Frodo, and Aragorn) between series A and B.

Although the short-term SSI is significant as a main effect and is involved in only one interaction, this also appears to be largely an artifact of the long-term SSI. Gala and Varda took more white mice than expected in all four series and thus selected short-term SSI mice about one-half of the time; indeed the total selection for SSI mice by these two birds (series A, D) is only six mice different than the total selection for non-SSI mice (series B, C). The strong preference for short-term SSI mice (white) shown by Gandalf in series A, his dramatic shift to gray (short-term SSI) mice in series B, and his relatively weak total selection for gray (non-short-term SSI) mice in series D contributed markedly to the effect of the short-term SSI on the total variance. Frodo's shift, although of lesser magnitude, also contributed considerably to the variance associated with the short-term SSI. Both birds took more mice of the short-term SSI color than the other color in three of four series, and showed only a weak overall preference for the non-short-term SSI color in the fourth series.

The difference between tests, beginning with negative values in tests 1 through 4 and switching to positive values in tests 6 through 9 (see totals, Table 8), seems to indicate a selection for odd, or uncommon mice as short-term SSI mice are common in test 1 and become less common through the sequence of tests. Most of the variance between tests again appears to be a function of the long-term SSI. In series A, the minus value for test 1 (Table 8) is largely the result of Aragorn's preference for gray mice that he maintained through most of series A (Table 3). In series B the minus values for tests 1 through 4 (Table 8) are primarily the result of the consistent preferences of Gala and Varda for white mice (Table 4). In series C most of the minus values for Tests 1 through 4 are due to the preference of Aragorn, Gala, and

Varda for white mice, a preference that prevailed through most of the series for all three birds. In series D most of minus value for test 1 was contributed by Gandalf who switched color preference in test 5 and made a sizable contribution to the positive values in tests 6 through 9 (Tables 6 and 8). Gandalf's performance in series D can only be interpreted as a preference for odd mice. Indeed Gandalf's performance in series B and C, as well as D, can be interpreted only as a reasonably strong preference for oddity. Frodo's performance in series A and B and Gala's performance in series A also seem to indicate a preference for odd mice.

In tests 6 through 9 the high positive scores in series A and B and the negative scores in series B and C (Table 8) can be attributed largely to the long-term SSI shown by various birds (Tables 3–6). The preferences for oddity shown by Gandalf, Frodo, and Gala, listed above, also contributed to these totals.

A number of other factors influences the kestrel's selection of mice. All birds showed a preference for taking mice from one or more pedestal positions. The kestrels tended to watch moving mice rather than stationary ones and probably took more of the former. A mouse facing the hawk was less likely to be attacked than one facing away. All of these variables were randomly distributed and serve only to reduce the effects of conspicuousness, the SSI, and, particularly, oddity. An odd mouse is less likely to exhibit a randomly occurring, attractive quality than a common mouse. In test 1, for example, a randomly occurring attribute would be nine times as frequent in common as in odd mice. In view of the factors that mitigate against the selection of odd mice in my experiments, it is surprising to find any evidence for the selection of odd mice.

DISCUSSION

Thus a long-term SSI is the most important determinant of prey selection in these experiments. Conspicuousness seems relatively unimportant. Several birds showed a distinct tendency to select odd mice, although this tendency was often obscured by the long-term SSI. I believe the tendency to select odd mice is nonetheless important. In nature "odd" animals would be much less common than in my experiments. A tendency to select odd prey thus might result in the capture of all of the odd animals in the environment.

It is perhaps not surprising that conspicuousness was relatively unimportant in influencing prey selection in my experiments. Dice (1947) found that owls selected conspicuous mice in the laboratory only after some artificial "cover" was provided for the mice. Similarly, in field experiments Kaufman (1973) found that Loggerhead Shrikes (*Lanius*

ludovicianus) selected conspicuous mice only when the mice were released in reasonably dense vegetation or at a considerable distance from the shrike. My mice were presented at a short distance and without cover.

The SSI concept was originally formulated by von Uexküll (1934) but it was Tinbergen (1960) who recognized its importance in the behavioral ecology of predators. In an often overlooked paper, on bird predation on insects, Swynnerton (1919) essentially came to the same conclusions as Tinbergen, but did not describe the concept of an SSI explicitly. As Landenberger (1968) noted, it is unfortunate that Tinbergen was never able to develop this interesting idea fully. Although he completed the manuscript of his 1960 paper before his tragic death, there is evidence that he was uncomfortable with at least several portions of it (Baerends and de Ruiter 1960). In recent years several critiques of Tinbergen's hypothesis have appeared, but in my opinion these do not contest effectively the basic principles of the SSI hypothesis. I cannot agree with Landenberger that the hypothesis is stated in such broad terms that it can be made to fit any observation and thus cannot be tested properly. This critique may hold for most ecological data but is untrue for behavioral experiments, where prey selection is actually observed rather than inferred from population and mortality counts. Dawkins (1971), although she presents excellent experimental data for the existence of an SSI in domestic chicks, argues that the SSI has been used in too many ways to be a useful term. However any more restrictive label would soon come to be used more broadly and in a few years would become similarly "useless." Royama (1970) presents an extremely detailed critique of Tinbergen's hypothesis and offers an alternative hypothesis of "profitability" in which a predator tries constantly to maximize its hunting efficiency. Smith and Dawkins (1971) agree with Royama in that they believe there is no good direct evidence for the SSI hypothesis and that the profitability hypothesis is a simpler one. However Croze (1970), dismisses Royama's criticisms in a lengthy discussion of which only a brief summary need be presented here. First I believe there is good experimental evidence for the existence of an SSI (e.g. Allen and Clarke 1968, Croze 1970, Murton 1971, Dawkins 1971, Smith and Dawkins 1971, Kaufman 1973, and this paper, to cite only some of the more recent contributions). What is lacking is unequivocal data from observations in nature. Indeed the existing observational data offer no better support for Royama's hypothesis than for Tinbergen's.

Royama argues that Tinbergen's SSI hypothesis is inadequate to explain selection at high prey densities, but Tinbergen suggested that predators need variety in their diet and hence do not prey exclusively

on one species. Royama argues that his profitability hypothesis can explain less than anticipated selection at high densities, but this is true only if one assumes it is more profitable for the birds to prey on other species; no direct evidence exists. Both Royama (1970) and Smith and Dawkins (1971) criticize Tinbergen's hypothesis for not taking into account observations that predators do not search the environment randomly. Tinbergen was well aware of this phenomenon (see Tinbergen 1960, Mook et al. 1960) but neglected to emphasize it in his description of the SSI.

The differences between Tinbergen's (1960) SSI hypothesis and the profitability hypothesis of Royama (1970) are not great, and most pertinent data could be used in support of either idea. If one interprets Royama's hypothesis as strictly and narrowly as he does Tinbergen's, then one is led to ask: Is it simpler for a bird to evaluate constantly the efficiency of a given search strategy and the availability of all species of prey than it is for a bird to have one or several SSI's and a tendency to vary its diet? It would seem that Tinbergen's hypothesis is simpler than Royama's.

My belief in the validity of the SSI as opposed to the profitability hypothesis, particularly in the contention "that the birds perform a highly selective sieving operation on the visual stimuli reaching their retina" (Tinbergen 1960), is reinforced by the following observations: one of my hawks, Gandalf, would occasionally approach mice indirectly instead of the direct attack shown by other birds. Gandalf occasionally landed on the pedestal next to the mouse he was intent on. In many of these cases the hawk and a mouse shared the pedestal for a few seconds before Gandalf continued his attack on the adjacent mouse without the hawk showing any sign of being aware of the mouse on the pedestal with him. In other cases the mouse sniffed or otherwise made contact with Gandalf and he invariably flew off and landed in some distant point of the room, obviously frightened by something of which he seemed unaware. In a few cases Gandalf landed on the mouse and seemed to be frightened off when the "perch" moved. These incidents were particularly dramatic when the mouse selected as prey was inconspicuous and the unnoticed mouse was conspicuous. The most conservative analysis of these results is that Gandalf was so intent on a particular mouse that he did not see the other. As the other mouse was never of the SSI color we can perhaps generalize that the bird could not readily detect this other mouse color, implying some type of stimulus filtering or some nervous mechanism that directs the bird's attention to only a part of the stimulus configuration. It should be unnecessary to point out that the above observations are somewhat difficult to fit into Royama's (1970) profitability hypothesis.

Other studies have produced data that at least suggest the existence of an SSI in hawks and falcons of various species. Uttendorfer (1939, 1952) and Rudebeck (1950–1951) have shown that individual hawks of several species show pronounced, and sometimes exclusive, preferences for a given prey species. In 20 years of trapping raptorial birds I have noted that it is difficult to attract hawks to traps baited with prey that is not that hawk species' normal food at that particular season, while in other seasons the hawks are easily trapped with the same species of prey. Brüll (1937) has indicated that it is easy to train a captive hawk to prey upon a single species. Falconers speak of "entering" their birds to a given species of prey, and with proper training Golden Eagles (*Aquila chrysaetos*) can be trained to attack and kill such unlikely prey as wolves. I suspect that much of the prevailing picture we have of extremely varied diets in raptorial birds may be the result of grouping data from individuals and seasons, and thus obscuring individual SSI preferences.

The evidence for the selection of odd prey in my experiments, although not so striking as the evidence for the SSI, is perhaps more interesting. Salt (1967) suggested that a preference for oddity is the one generalization that encompasses a great variety of experimental results and observations of predation. However the unequivocal evidence for the selection of odd prey, independent of other factors, is exceedingly limited; indeed, it may be limited to my data, and perhaps those of Pielowski (1959, 1961). Apostatic selection, which may operate in the maintenance of polymorphic prey populations (see e.g. Clarke 1962, Elton and Greenwood 1970) may be incompatible with selection for oddity. The concept of apostatic selection is based on observations that thrushes tend to prey preferentially on the most abundant color morph of snails of the genus *Cepaea*. However Carter (1967) showed that conspicuousness is important in thrush predation on *Cepaea* and that apostatic selection does not appear to be operative in at least several populations of snails.

The selection of odd mice in my experiments may be the result of a tendency of the kestrel to vary its diet (Tinbergen 1960), or a response to novelty (Berlyne 1960). Some birds showed a tendency to select a reasonably constant proportion of mice of a given color throughout a series (e.g. Gandalf, Gala, Varda in series A) regardless of the relative abundance of the mouse, suggesting that the bird seeks a fixed amount of novelty or variety. Still, not all birds showed this response in a given series and no bird maintained such a level of preference throughout the four series. Regardless of the label and the implied explanation of the behavior, the preference for oddity continues to have the same ecological and evolutionary implications.

In most prey populations, odd prey is probably unfit, at least if one confines the idea to within-species variation, because common prey must be adapted to the environment or it would not be common (Hoffman 1964). Experimental evidence shows that predatory fish catch a disproportionate number of crippled prey (Popham 1943, Ricker 1949, Ivlev 1961) and quantitative field data suggests that predatory birds catch a higher proportion of diseased, crippled, or otherwise abnormal prey than reasonably might be expected to exist in the prey population as a whole (Rudebeck 1950–1951, Van Dobben 1952, Burckhardt 1953). As unfit animals are probably easier to capture than fit animals, this type of evidence may simply indicate the relative success of the predator, not the selection of unfit prey. Eutermoser (1961) found that 40 of 100 Carrion Crows (*Corvus corone*) taken by his trained Peregrine Falcons (*Falco peregrinus*) suffered from some obvious handicap. A sample of 100 crows shot included only 23 with obvious handicaps. Lack (1966) found that 3.1% of Wood Pigeons (*Columba palumbus*) that were shot were diseased while only 1.6% of those captured with narcotic baits were diseased. Thus a sample of shot birds contains more unfit animals than the population as a whole, suggesting that: (1) Eutermoser's falcons were taking an even higher proportion of unfit birds than his study indicated and (2) selection was not involved, but that the data simply indicate the relative vulnerability of prey as the gunner was not selecting diseased birds. Some of Ivlev's (1961) experimental data also support the hypothesis that crippled prey are simply more vulnerable to predation and that selection by the predator may not be involved.

At least several dozen anecdotal accounts have been published that seem to indicate active selection of unfit prey by the predator (see Rudebeck 1950–1951, Mossman 1955, Curry-Lindahl 1964 for a listing of many of these references). Many of the examples involve birds of prey. These observations lack controls; a predator usually selects an individual out of a flock or group but the observer may only note the cases where the individual is unfit. It may be that the selection of unfit individuals is no greater than their frequency in the prey population.

The presumed attractiveness of abnormal behavior of prey to predators has been invoked as an explanation for the evolution of distraction displays (Cott 1940). Berger and I have designed and operated successfully a variety of hawk traps based on the assumption that abnormal prey behavior is attractive to hawks (see Bub 1968 for a description of these techniques). Several students of predation believe that predators carefully evaluate their chance of capture with each prospective prey item (e.g. Cushing 1939, Errington 1967, Cade 1967) and hence would select unfit prey. The experiments of Sparrowe (1972) also offer indirect

support for this idea. Slobodkin (1968) showed that it is to the predator's advantage for it to select as prey those individuals that will not contribute to the growth of the prey population. It is possible that predators act as "managers" of their prey (cf. Blondel 1967; Errington 1963, 1967) or, to state this in another way, that the predator-prey system evolved towards maximizing yield. Similar principles of "optimality" have proved useful in analyzing the interactions in a variety of biological systems (see e.g. Rosen 1967). Pimentel (1968) found that a laboratory host-parasite system exhibited evolutionary changes after only relatively few generations. The modifications in both the host and parasite were believed to be the result of "genetic feedback" from the other species of the system. The concept of the evolution of the community probably was first stated in detail by Emerson (1949).

Thus there are strong theoretical arguments for the selection of "odd" or "unfit" prey and the concept has won wide acceptance from biologists. The paucity of unequivocal data is perhaps surprising and is an indication of the difficulty of gathering information on this fascinating idea. Further experiments are in progress in my laboratory, involving predators that encounter their prey singly instead of in groups, systems involving several species of prey, and the selection for unfit prey.

SUMMARY

Five tamed American Kestrels were offered a choice of varying ratios of gray and white mice on white or gray substrates. The results indicate that the specific searching image (Tinbergen 1960), a tendency to continue to select a given type of prey, is the most important factor influencing prey selection. Conspicuousness of prey is relatively unimportant. There was also a tendency to select odd prey, prey that differed in color from the majority of animals offered to the kestrel. This latter tendency could contribute to the selection of unfit prey and have important implications for the ecology and evolution of both prey and predator.

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