FACTORS INFLUENCING DIFFERENTIAL PREDATION ON HOUSE MOUSE (*Mus musculus*) BY AMERICAN KESTREL (*Falco sparverius*)

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ABSTRACT - Due to the sexual size dimorphism of raptors, it was thought that a preference for different sized prey might be evidenced between male and female American Kestrel (*Falco sparverius*). A modified bal-chatri trap was used which gave kestrels a choice of 2 types of mice. In the first experiment, wild birds in the field were given a choice between a large mouse (35 - 40g) and a small mouse (22 - 27g). The results of the summer season were compared to those of the fall-winter season. The preferred prey size between the males and the females was not significantly different in fall-winter (X^2 = 0.036, P $>$ 0.05). During breeding season, the preferred prey size shifted dramatically; males chose predominately small mice, females predominately large ones ($X^2 = 20.55$, P $<$ 0.001). The second experiment showed the influence of hunger on preference for a particular sized mouse. The birds that were determined to have a higher hunger level chose predominately the large mice ($X^2 = 5.18$, P $<$ 0.025). The third experiment showed the effect of a conspicuous, but odd, color of prey (white mouse) compared to that of the normal, agouti color. The agouti color was chosen by 82% of the birds. The difference between the actual preference and a random choice was highly significant ($X^2 = 18.85$, P $<$ 0.005).

There are many aspects to the selection of prey by predators. Lack of protective coloration (Dice 1947; Kaufman 1974a), prey activity (Kaufman 1974b) and oddity (Mueller 1971) play important roles. The roles of predator experience (Mueller and Berger 1970), specific search image (Tinbergen 1960; Mueller 1971) and hunger (Mueller 1973) have also been demonstrated. Several authors have investigated the role of size in the selection of prey by storks (Ogden et al. 1976), shrikes (Slack 1975) and several species of raptors (Storer 1966; Mueller and Berger 1970; Synder and Wiley 1976; Marti and Hogue 1979).

The American Kestrel (*Falco sparverius*) shows only a slight size dimorphism with the male being, on the average, 8% smaller by weight than the female (Brown and Amadon 1968). The kestrel must select prey with an efficiency such that the energy expended to find, catch and kill the prey is less than the energy obtained. Predation efficiency is even more important during the breeding season when the male feeds the female and young, as well as himself. Certain prey must exist that are more efficiently found and subdued (Emlen 1968). One aspect of this efficiency is size of prey. This study attempts to show a preferred size of prey by kestrels which corresponds to the sex of the bird, hunger of the bird and color of the prey, as well as seasonal variation.

METHODS AND MATERIALS

A modified bal-chatri trap (Mueller and Berger 1959), consisting of 2 compartments (each 13 cm x 25 cm) separated by 15 cm and made of ½-in hardware cloth was used. Capture loops were made using 12# + cst monofilament line with approximately 20 loops attached to each compartment. Two size categories of the agouti colored House Mouse (*Mus musculus*) were used: large (35-40g) and small (22-27g). All agouti mice were inbred genetic strain *C2H*. Small mice were randomly placed in 1 cell and large in the other. Whenever possible, the 2 mice used had a 15g weight difference. When a perched kestrel was sighted the trap was tossed to the ground from a slowly moving vehicle at a distance of 10-40 m from the bird. The trap was removed after 5 min unless some type of response from the kestrel was observed. When the bird was trapped, its sex was noted as well as which mouse (large or small) it attacked. Any time a bird switched from one side of the trap to the other, the trial was discounted. This happened on only 10 of 149 trials and only in the fall-winter season. The fall-winter season included the months September, October, November and December 1980 & 1981. No switches were made during the summer season of May, June and July, 1981, 1982, 1983 (see Tables 1 and 2). Males and females were compared for prey size preference as well as difference between the 2 seasons. Independent and semi-independent young birds were separated from adults on the basis of whether flight feather molt was occurring during the breeding season (see Table 2). During fall-winter season the immature birds were combined with the data for adults.

A second part of the study concerned the determination of hunger in birds which might have influenced preference for a particular sized mouse. Hunger was determined by computing ratio of average wing chord to the cube root of average body wt. Any bird with a ratio above the average was considered underweight and any bird with a below average ratio was considered overweight. Overweight and underweight kestrels were then sub-

Table 1. Comparison of the number of female and male kestrels that chose either the large or the small mouse during the fall-winter "season". The category "switched mice" denotes that the kestrel attacked one size mouse and then switched and attacked the other.

	LARGE MOUSE	SMALL MOUSE	SWITCHED MICE
Males	23	26	4
Females	41	49	6

Table 2. Comparison of the number of female and male kestrels that chose either the large or the small mouse during the "summer" season. The category "switched mice" denotes that the kestrel attacked one size mouse and then switched and attacked the other.

	LARGE MOUSE	SMALL MOUSE	SWITCHED MICE
Males	5	23	0
Females	21	4	0
Immature Females	3	10	
Immature Males	1	1	0

jected to Chi-square (X^2) analysis to determine if both preferred the same or different sized mice.

Finally, I determined if a conspicuous, but odd-colored, mouse (white) was preferred over the more natural color (agouti). The white mouse could be seen, when it moved, up to approximately 300 m away, whereas the agouti mouse could be seen up to approximately 200 m. These distances were determined by objective analysis by the author. The background did not appear to make much difference in discerning the white mouse unless the substrate was very light in color. The experiment was similar to the large and small mouse experiment, except the trap contained only 1 white and 1 agouti mouse with no more than 3 g difference in wt.

Comparison of wing chord was done between summer and fall-winter kestrels to determine if 2 populations of kestrels (migratory and non-migratory) were being sampled in fall-winter versus 1 population in summer (non-migratory). A t-Test was used to compare means and a F-test for variance.

RESULTS AND DISCUSSION

Fifty-three adult birds were trapped during the summer season when young were in the nest or still on the territory being fed. In the fall-winter season 1980 and 1981, 149 birds were trapped. Eighty-nine birds were trapped for the white mouse/agouti mouse experiment in the fall-winter season, 1982 and in January 1983. Kestrels were trapped in open habitat in Los Angeles, Orange, Riverside and Kern counties, southern California. During fall-winter, more females were trapped than males. This may have been due to sexual habitat preference (Koplin 1973). Females tend to prefer open habitat while males prefer woodland margins.

The data are shown in Tables 1-5. The preferred prey size between males and females was not significantly different in fall-winter ($X^2 = 0.036$, $P > 0.05$; see Table 1). During the breeding season, preferred prey size shifted dramatically; males predominately chose small mice, females predominately large mice (see Table 2). This difference was highly significant ($X^2 = 20.55$, $P < 0.001$) and was reflected in seasonal comparisons within each sex. Males shifted from a random choice in fall-winter to a strong preference for small mice in the breeding season ($X^2 = 5.32$, $P < 0.025$). Females shifted from a random choice in fall-winter to a strong preference for large mice in the summer season ($X^2 = 10.14$, $P < 0.001$).

Table 3. The number of overweight and underweight females that chose either the large or small mouse during the fall-winter "season".

	LARGE MOUSE	SMALL MOUSE
Overweight	12	13
Underweight	11	13

Relationship of hunger to preferred prey size was apparent with females. During the fall-winter, underweight females predominately chose the large mouse while overweight females chose the small mouse (see Table 3). This difference in the preferred prey size was significant ($X^2 = 5.18$, $P < 0.025$). However, there seemed to be no relationship of hunger to preferred prey size in males ($X^2 = 0.018$, $P > 0.05$) (see Table 4). Average wing chord for 49 males and 90 females was 188 mm and 196 mm, respectively. Wing chord means and variance values did not differ significantly from summer to fall-winter seasons (t-Test, $P > 0.05$; F-test, $P > 0.05$). Average weight was 108 g for males and 122 g for females.

Table 4. The number of overweight and underweight males that chose either the large or small mouse during the fall-winter "season."

	LARGE MOUSE	SMALL MOUSE
Overweight	12	13
Underweight	11	13

Effect of a conspicuous, but odd, color of prey (white mouse) is seen in Table 5. There was no significant difference between male and female selection for color ($X^2 = 0.272$, $P > 0.05$), therefore they were combined. Eighty-two percent of kestrels chose agouti mice. The difference between the actual preference and a random choice was highly significant ($X^2 = 18.85$, $P < 0.005$).

Table 5. The number of males and females that chose either the white or agouti colored mouse during the fall-winter "season". The category "switched mice" denotes that the kedtrel attacked one size mouse and then switched and attacked the other.

	WHITE	AGOUTI	SWITCHED MOUSE
Males	4	26	1
Females	12	47	2

Behavior of kestrels toward the trap led me to believe that each bird was preferentially selecting one of the mice. The kestrels exhibited several types of behavior. In one type the bird flew toward the trap and hovered over it for several seconds before attacking one side. In another pattern the kestrel flew to a position over the trap (telephone lines or poles, trees, etc.) and sat examining the trap for some time before attacking. In the third, and most convincing, type of behavior, the bird was not caught on initial attack, flew away, and consistently returned to attack the same mouse. This pattern continued until the kestrel either was caught or gave up. In the last, the bird attacked one side of the trap, then attacked the other or it attacked one side, flew away, and returned to attack the other. This was rare, occurring 6.7% of the time, during fall-winter and was excluded from data analysis.

The results clearly show a preference for size of prey in spring for kestrels. The reasons for this preference are not as clear The first possible reason was advanced by Storer (1966). He hypothesized that due to sexual size dimorphism, sexes take different size prey serving to reduce competition between them so that the pair can feed in a smaller territory. This may work well when the prey is birds. Young birds (after fledging) are essentially the same size as adults, so preying on different size birds means preying on different species. This would seem to reduce competition between sexes and increases the number of potential prey. However, in rodent species young are smaller than adults. Preying on different sizes (hence difference ages) of the same species would not seem to increase available prey, although it would allow some reduction in competition between sexes. If male and female kestrels prey on different sizes of the same species, the prey population would be reduced as quickly as if both sexes preyed on both sizes equally. This hypothesis should not be quickly discarded, however, as even a subtle avoidance of competition is an advantage.

An alternative is that males chose the smaller mouse because there are simply more small mice at that time of the year. The males may have formed a specific search image (SSI) for smaller mice on the basis of availability. The females, on the other hand, do little hunting for much of the season and may not have a strong SSI formed and thus choose the larger mouse for a larger reward.

Another alternative deals with the energetics of carrying a mouse to the nest cavity. The female does little hunting for most of the breeding season while the male procures food for himself, the female and young. He must carry prey to the nest for distances up to 1 km (Balgooyen 1976). It may be less energetically demanding to carry more small mice to the nest than fewer large mice. The female, on the other hand, hunts infrequently near the nest, and does not have far to carry prey; therefore, it seems most advantageous for her to attack the largest prey possible. Studies of the energetics of flying with varying weights are needed to confirm this hypothesis.

During winter, the males and femals are feeding only themselves and would not need to be as selective with the size of prey. The prey does not have to be carried far and both sexes should be able to kill the large category mouse with almost equal skill. Males do not have the same bulk as females, however males do have a lighter wingloading and feet and beaks which are not significantly different in size (Balgooyen 1976). The male should be able to transport prey as easily as the female due to lighter wingloading. The only advantage seems to be that females have more bulk to subdue larger prey. A flaw in this hypothesis is that it would seem most advantageous to prey on the largest mouse because of the larger gain. This was not, however, indicated by the data. The birds selected a large proportion of small mice in winter. This may be explained by the hunger of the bird. A kestrel that is underweight might be more inclined to attack a larger mouse than a kestrel that is overweight.

The influence of hunger in predation was shown by Mueller and Berger (1970). They trapped Sharp-shinned Hawks (*Accipiter striatus*) in 2 manners. One in which the hawks actually struck lure birds [pigeons, starlings or House Sparrows (*Passer domesticus)*], and the other in which the hawks flew near, but did not attack, and were trapped in a net. Although the data were not statistically significant in all cases, a tendency existed in which lighter hawks actually struck prey more frequently. This suggested to them that hunger influences a hawks tendency to kill. Mueller (1973) demonstrated the relationship of predatory behavior to hunger in American Kestrels. Kestrels were deprived of food for intervals of 1, 5, 10, 20, 25, 30 or 35 h. In his experiment on deprivation interval to food consumption the curve was almost linear. On the average, kestrels consumed 2% of their body wt after 1 h of deprivation and about 13% after 35 h. In the experiment on deprivation interval to killing tendency the curve was only a little less linear. After 1 h of deprivation kestrels killed mice 14% of the opportunities and 92% after 35 h. Mueller (1973:519) felt that all his data "indicate a complete correlation between food consumption and predatory behavior, suggesting that predation is a direct response to hunger."

In this paper it was assumed that an underweight bird is more hungry than an overweight bird. The effect of hunger is seen in Tables 3 and 4. Table 3 shows the effect of female hunger in which 32 of 48 (67%) of the overweight females chose the large mouse. Table 4 shows this not to be the case with males. There is no difference in preferred prey size from underweight to overweight males. There may be other factors that override the effect of hunger in males. The data for females suggest that hunger influences the selection for prey, which is contrary to Lorenz's (1966) generalization that killing instinct of predators is unitary and driven independently of hunger. However, my study supports the contention of Mueller (1973) and Mueller and Berger (1970) that hunger plays an important role in the tendency to kill.

The results of the white mouse/agouti mouse experiment clearly show a preference for the natural agouti color although there is a definite selection for the odd color (white) at times. This was especially evident when kestrels attacked the white mouse, was not caught, and returned to the same mouse before getting caught. The selection of agouti mice seems to show an SSI for agouti color whereas the selection of white mice may show a tendency of a kestrel to vary its diet (Tinbergen 1960; Mueller 1974). I believe the existence of an SSI is supported by this study, although there appear to be many variables that can alter the SSI. Several authors believe that predators carefully evaluate their chances of success with each prospective prey (Cushing 1939; Errington 1967; Cade 1967). When this evaluation encompasses the SSI, the predator will decide whether to attack or not (e.g., if the mouse is the correct size, color and species but the distance to the prey is too far and the cover is too dense, the bird will not attack).

The selection of odd mice in my experiment is consistent with the results of Mueller (1974:716) in which "some birds showed a tendency to select a reasonably constant proportion of mice of a given color throughout a series regardless of the relative abundance of the mouse, suggesting that the bird seeks a fixed amount of novelty or variety." Mueller contended that in most prey populations odd prey is probably unfit and, therefore, would be actively selected from the environment (see Mueller 1974 for a listing of references to support the contention).

There are inherent problems in any study that attempts to relate an artificial situation to the real world, and this study is no exception. A choice between 2 mouse sizes probably rarely occurs in nature and it seems unlikely that the kestrel would not kill a mouse of the non-preferred size. However, the birds probably have an SSI for a preferred size and when all factors are considered (i.e., distance from prey, visibility of prey, etc.) they are more likely to attack the preferred size than another. This does not mean that either sex will not attack the non-preferred size mouse. The kestrel is an opportunistic predator and will attack anything within certain broad limits. It does mean that they have an SSI for a size prey that they will aggressively pursue over long distances and more adverse conditions than other size prey. Another problem to consider is the activity of the 2 mouse sizes, as Kaufman (1974b) showed that active rats were preyed upon more than inactive rats. Marti and Hogue (1979) found that small mice may move faster than large mice, but they do not move longer distances in the same time period. If the kestrels preferred a faster (smaller) mouse or a slower (larger) mouse, it would not be expected that they would switch this preference seasonally as is the case in this study.

A third potential problem is with fall-winter data which dealt with hunger in females where 2 populations of females were sampled (migratory and non-migratory). Although wing chord analysis showed no difference in the size of these 2 populations, it may be that migratory females are, on the average, lighter in wt than non-migratory females. Migratory females may have a previous SSI formed for large mice. This would bias the data toward the results achieved based on hunger. In the fall-winter data, part of the population were immature birds which were not distinguished from adults. Mueller and Berger (1970) showed that inexperienced raptors tend to take inappropriate prey. However, I have a strong feeling that by winter young birds have formed an SSI.

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