PREY-CATCHING BEHAVIOR IN THE AMERICAN KESTREL (FALCO SPARVERIUS)

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ABSTRACT

PREY-CATCHING BEHAVIOR IN THE
AMERICAN KESTREL (FALCO SPARVERIUS)

By

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Since survival of a predator depends on its behavioral capacity to respond to a variety of prey-capture opportunities, it is important to identify the behavioral mechanisms involved in capturing prey. Three hand-reared and 12 wild-trapped American kestrels (*Falco sparverius*) were trained through a reward system to catch a mouse-like prey model. Duration of prey exposure to kestrel, contrast of prey to background, and density of cover shielding prey were varied experimentally to determine: 1) how kestrels respond to opportunities to catch prey; 2) effects of experience on prey-catching abilities of kestrels; 3) effects of prey exposure, prey contrast, and density of cover on prey-catching success in kestrels; and 4) the relationship between experimental results and field observations of prey-catching by wild kestrels.

When kestrels detected prey, some minimum duration of exposure of prey provided a stimulus threshold which induced an attack. If the stimuli were maintained during the attack it was carried to completion. Young and adult

kestrels differed little in physical ability to capture prey once an attack was started. Ability to recognize a promising prey-capture opportunity apparently develops with experience. The three hand-reared kestrels became highly conditioned to the test system and reacted "automatically" to prey movement and attacked in situations wherein no wild-trapped kestrels would make attempts. In contrast, wild-trapped birds "looked over" each experimental prey-capture opportunity before attacking. Duration of prey exposure affected number of attempts and successes more than prey contrast or cover density throughout testing. Combination of dense cover with low prey contrast resulted in reduced number of attempts and success. These and other influences on a prey-capture attempt control the relative amount of exposure of the prey item to the kestrel by obscuring it or making it less conspicuous. The length of time prey is exposed to the kestrel controls whether or not an attack is started, whether it is carried through, and ultimately whether a capture is made.

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By

Rollin DeMers Sparrowe

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INTRODUCTION

Proficiency in capturing prey in a variety of environmental situations is essential for the survival of a predator. Among vertebrate predators, prompt responses to changes in prey availability depend upon development of appropriate behavioral mechanisms for use in catching prey. Behavioral responses to prey by avian predators depend upon their: 1) perceptual abilities in locating prey, and 2) physical abilities in reacting to and catching prey. Vegetative cover, concealing coloration of prey, and characteristics of prey movement, contribute to success or failure in catching prey and can be varied experimentally to examine prey-catching proficiency.

Experiments with owls (Dice 1945, Payne 1962) indicate that prey-catching mechanisms involve perceptual abilities capable of a high level of discrimination. The swift recognition of prey or a prey-catching opportunity necessary for success in attacks at mobile prey may be aided by formation of a "specific searching image" of prey (Tinbergen 1960). This image may avoid time-consuming evaluation of each prey-catching opportunity, and allow a raptor to specialize in certain prey items which afford the greatest return per unit effort (Emlen 1966, MacArthur and Pianka

1966). Prey-catching abilities in raptorial birds have not been described, but field studies by Rudebeck (1950), and Craighead and Craighead (1956) indicate that raptors miss far more prey than they catch.

This study is based on more than 6000 capture attempts by 17 wild-trapped and 3 hand-reared sparrow hawks, or American kestrels, (*Falco sparverius*) trained to catch prey models in the laboratory. Duration of prey exposure, contrast of prey to background, and density of cover shielding prey were varied experimentally for the following objectives:

1) to determine how kestrels respond to opportunities to catch prey by measuring a) their abilities to detect prey and recognize favorable opportunities, and b) their abilities to react to and capture prey;

2) to determine the effects of experience on prey-catching abilities by comparing a) performances of totally inexperienced and experienced kestrels, and b) performances of kestrels before and after controlled experience;

3) to determine effects of prey exposure, prey contrast, and density of cover on prey-catching success in kestrels; and

4) to relate experimental results to field observations of prey-catching by wild kestrels.

REVIEW OF LITERATURE

Investigations into the nature of predator-prey interactions have concentrated on food habits (e.g. Errington et al. 1940), or fluctuations in populations of predator and prey (e.g. Huffaker 1958), and have largely neglected examining the ways in which predators catch their prey. Since survival of a predator depends on its behavioral capacity to respond to a variety of prey-capture opportunities, it is important to identify the behavioral mechanisms involved in capturing prey.

Most resources, including food, are not equally distributed but appear in clumps or patches in the environment. Since related species cannot compete directly for resources and survive (Gause's Law), they differ by using habitat in specialized ways (MacArthur and Levins 1964). Species which spend their time searching for small food items, like seed-eating birds, cannot afford to overlook many food items and will utilize resources in proportion to their availability. Pursuing species, like some raptors, which catch large food items, can efficiently specialize and use only a single resource. MacArthur and Pianka (1966) similarly conclude that the more productive environment should lead to restricted diet in terms of number of species eaten. The implication is that, in a productive environment, a predator will be able to specialize and utilize an optimal diet yielding greatest possible energy return for energy expended in a prey capture. Emlen (1966) has further described a model which relates optimal food preference and caloric yield per unit time, illustrating an energy/effort relationship in food getting.

Schoener (1969) presents models to predict optimal size for several types of predators on the basis of how they locate and overtake prey, and how they utilize their feeding time. He divides predators into those which spend time and energy in pursuit, handling, and eating prey, but not in search ("pure pursuers"), and those which spend time and energy in search, handling, and eating, but not in pursuit. Schoener makes a series of predictions based on his models, agreeing with MacArthur and Levins (1964) that efficient pursuers, like many raptors, can afford to specialize in prey items. Schoener (1969) uses raptors as examples in his models, but since prey-capture opportunities vary greatly, most raptors may at one time or another fall into each of Schoener's categories.

Perceptual and discriminatory needs of a predator are exacting in a complex environment with many potential prey species. Roeder (1959) suggests a selective advantage for short time intervals in prey recognition and predator attack. He says that a predator reacts to mobile prey in two stages: 1) stalk, detection, identification, and orientation to the prey; and 2) speedy attack steered by detailed information gained in the first stage. If step one were required for each prey item, the predator would be constantly sorting out detailed information about each potential prey. Tinbergen (1960) hypothesized that predators may overcome this difficulty by going through step one only during the first series of encounters with a specific prey, forming a "specific searching image" of prey. Tinbergen further hypothesized that birds would not accept a prey unless they have acquired the appropriate "image" and that they acquire it from frequent chance encounters. Gibb (1962) suggested that the search image may break down when prey are very abundant, and that birds acquire it only at a certain prey density threshold.

Perception of prey may be accomplished by a variety of highly discriminatory mechanisms. Solitary wasps (Philanthus bicinctus) select prey within very narrow size ranges by using visual and tactile cues (Mason 1965). Small mammals may use olfactory and auditory stimuli to select insect prey (Holling 1956, 1958). Dice (1945) found that owls used vision to locate dead prey at low light intensities, selecting conspicuous mice over conceal-ingly colored mice more than would be expected by chance. Payne (1962) demonstrated that barn owls (Tyto alba) are capable of locating prey by auditory mechanisms in total darkness and striking with an accuracy of one degree of angle in horizontal and vertical planes.

Among the best known discriminatory mechanisms in perception and location of prey by a predator is echolocation in bats. Gould (1955) postulated that insectivorous bats probably caught prey by locating, pursuing, and attacking them directly, rather than by random feeding. Insect-eating Myotis were studied by Griffin et al. (1960) who divided prey capture into search, detection, approach, and terminal phases. The entire sequence usually occurred within about 1/2 second of prey detection, and up to 20 fruit flies or 9.5 mosquitoes were taken per minute. Bloedel (1955) experimented with fish-eating bats (Noctilio leporinus) and calculated a formula for expected success due to random dipping. His trials with trained bats showed that they did not catch more fish than expected by chance, and that bats caught more prey when prey were denser - further evidence of randomness. Intensive experiments with Noctilio by Suthers (1965) revealed that bats located prey below the water surface by random dipping, but probably located fish in nature by disturbances made on the surface. Using a reward system to condition bats to grasp "prey", Suthers found that bats could distinguish wires as small as 0.21 mm diameter extending above the surface.

Bond (1936) found that both trained and wild falcons formed "prey-seeking habits" and confined their hunting to a single species or group as long as they could. He suggested that when a chosen food runs out a new prey item is selected and pursued, and that each new prey type must be learned. Cade (1955) experimented with winter territories of sparrow hawks and noted that certain birds repeatedly used the same hunting perches at the same time of day. Establishment of a feeding habit, including the use of favored perches and extensive hunting in certain fields in discussed by Craighead and Craighead (1956). They (p. 181) separated raptors into two groups largely on the basis of physical abilities, with "restricted feeders" being those able to catch only a few prey species (e.g. marsh hawk, Circus cyaneus), and "general feeders" being those physically able to take a variety of prey (e.g. horned owl, Bubo virginianus). Craighead and Craighead (1956) noted that general feeders may confine their predation to one or several prey species which form the largest prey populations.

Studies of food habits reflect changes in and responses to prey availability, and support models of MacArthur and Pianka (1966) and Emlen (1966) regarding optimal use of food resources on the basis of a maximum return for effort. In two Michigan winters (Craighead and Craignead 1956) Microtus and Peromyscus combined made up 85% and 93% of total diet of 5 kestrels, with birds being utilized up to 13% of the diet the first winter. Birds were by far the most abundant prey available but were little used - probably because they are hard to catch - suggesting again Emlen's "return-per-unit-effort" hypothesis for prey selection. Heintzelman (1964) similarly found Microtus the most common summer prey of kestrels, and noted that local prey populations largely determined summer food habits.

Characteristics of prey-catching abilities in raptors are treated in several field and experimental studies. Rudebeck (1950) observed 52 captures in 688 "hunts" for 7.6% success by 4 species of migrating raptors (including 2 falcons) along the southern coast of Sweden over a 5-year period. A hunt was an attempt at one prey individual, whether one or 40 "stoops" were made. He observed that the raptors were not highly specialized in their choice of prey during migration, but that most attacks were directed at other migrating birds rather than ground-dwelling prey. Craighead and Craighead (1956) observed hunting hawks over several years time and considered prey availability the dominant factor in hunting activities, concluding that raptors miss more prey than they catch. Baker (1962) recorded 1 capture in 43 attempts for a red-tailed hawk (Buteo jamaicensis) preying on bats leaving a cave.

The species chosen for this study, the American kestrel, was described by Bent (1938) as "a bird of open country and the borders of woodland and finding most of its food on the ground," with foods including insects, birds, mammals, reptiles, and amphibians. Life history information may be found in Bent (1938) and other general works on birds of prey, but there is surprisingly little literature on kestrels besides Cade's (1955) experiments on winter territories, the Craigheads' (1956) studv of food habits and movements, and Heintzelman's (1964) summer food habits work. Kestrels occur commonly in agricultural areas and even cities (Bent 1938), hunt mice in old fields and fencerows and grasshoppers in croplands, and are reasonably easy to approach and observe closely. For these reasons, and because they are relatively easy to handle and train, kestrels are very well suited for experimental studies and offer the best opportunity to study prey-catching mechanisms in a raptor.

METHODS

Field Work

Twenty kestrels were trapped with "bal-chatri" noose cages (Berger and Hamerstrom 1962) baited with deer mice (*Peromyscus* spp.) or meadow voles (*Microtus* spp.) in Clinton, Ingham, and Shiawassee Counties, Michigan, in 1968 and 1969. Traps were dropped from a moving auto in sight of the kestrel. I then watched from about 100 m away and moved in when the bird was snared.

Prey-catching attempts by kestrels were observed with binoculars from 50-100 m in conjunction with trapping. A prey-catching attempt consisted of a dive into cover or at prey. Where possible, sex and age of each kestrel were determined, captured prey were identified, and location, time of day, weather, cover being hunted, and hunting method were recorded.

Laboratory Procedures

Apparatus

Two rooms (2.5 x 4.9 x 3.1 m) opening to an enclosed hallway were used for holding and testing kestrels. The holding room contained two 3.1 x 0.9 x 0.8 m tables divided by 0.8 m-high partitions into eight, 0.8 x 0.9 m perch compartments with wood chips covering the bottom of each compartment. Perches were 8 mm diameter aluminum rods running laterally 15 cm high through the rear of each compartment. A 2.5 cm binder ring with a 60 cm leash secured each bird.

The test room (Figure 1) had a perch 2.1 m high at one end and a 0.6 x 2.1 m capture surface of black cloth on the floor of the opposite end. Air distance from perch to capture point was 4.3 m. A 2.5 x 8 x 1.5 cm lead-weighted, prey model filled with rubber foam and covered with cloth was drawn from right to left across the capture surface by a thread connected by pulleys to a motorized drum (Figure 1). Prey models started from a black paper tunnel on the right and disappeared into another tunnel on the left. A mercury switch outside the room controlled a 60 cycle Dayton electric motor with attached drums for varying speeds of prey movement from 62-124 cm/second. A linear measure marked in 5 cm intervals was placed beside the path of the prey.

Light reflectance of prey models was varied in relation to that of background cloth to get a precise measure of contrast. Light reflection of cloth dyed with Rit liquid black dye was measured by a sensitive darkroom light meter using a 60-watt bulb light source 36 cm above the cloth in a cardboard box. The light sensitive cell of the meter was 7.5 cm above the cloth at an angle of 35°. Black background cloth reflected 6% of incoming light,

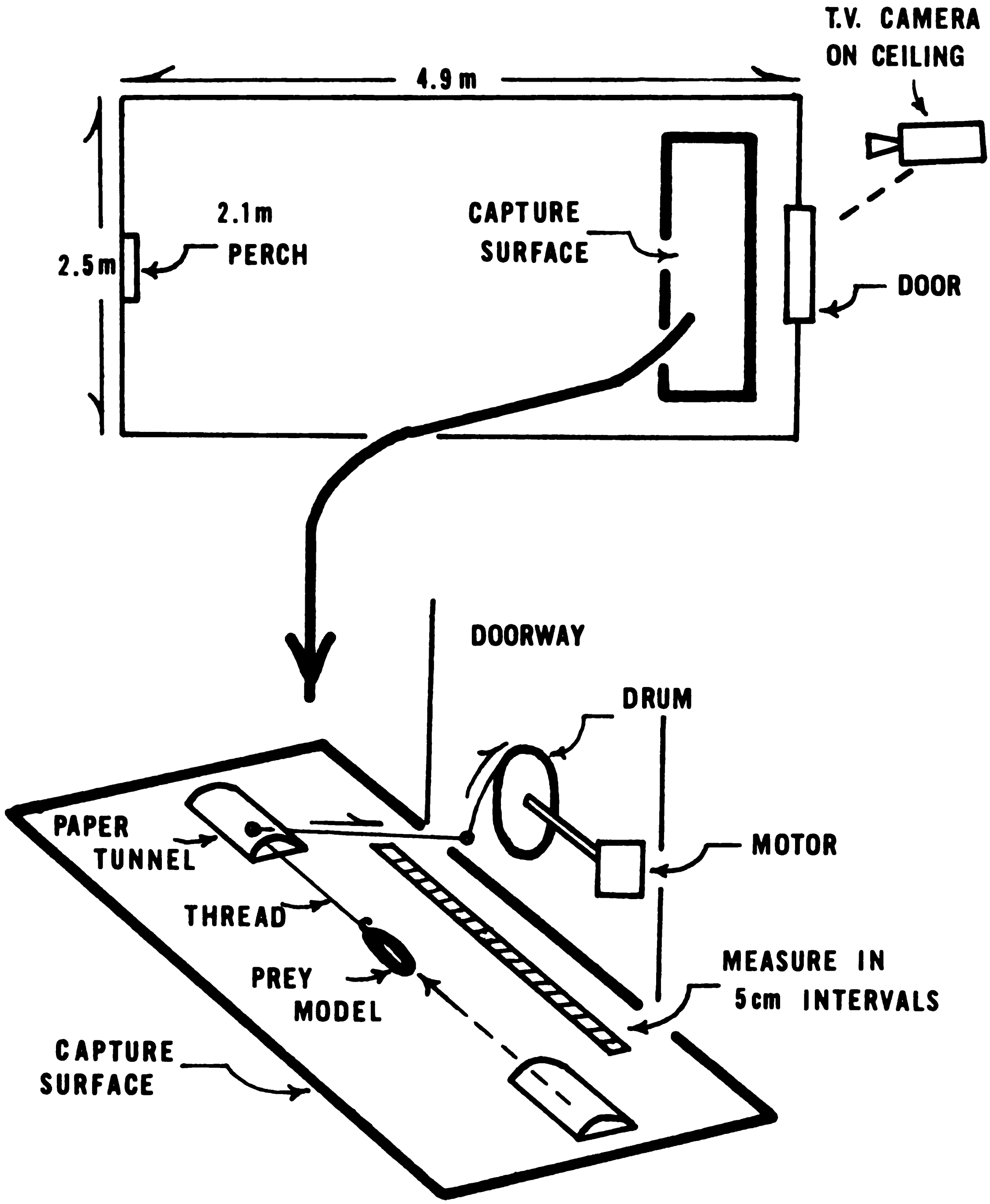

Figure 1. Organization of test room and apparatus for controlled movement of prey model.

whereas prey model cloth with 20% light reflectance was used in training models. Black paper tunnels placed over the path of the prey in some tests had two cm-wide strips left intact and cutout strips varied in size to obtain desired densities. Cover density tunnels were about 1 1/2 inches above the prey.

A Sony CV-2100 Videocorder closed-circuit television system was used to observe the capture surface and record and play back prey-capture trials. The camera was mounted on the ceiling 2.9 m above the capture surface, and monitor and videocorder were on a table outside the door at the capture end of the room.

Experimental Procedures

Newly captured birds were weighed, fitted with leather leg "jesses" (Beebe and Webster 1964:47), and attached by a leash to a perch compartment in the holding room. New birds were handled daily so they would stand upon the fist and be carried to be weighed and tested, and were entered into the prey-capture system by the following approximate training sequence:

Days	
0 - 7	orient to venison diet; feed from prey models.
8 - 12	initial "captures" of prey models in test room.
13 - 22	100 captures of prey models moving at 62 cm/second over 160 cm distance, 10/day.
23	begin regular testing.

A feeding regime was used to maintain condition and control hunger in test birds. Training and testing were done at approximately the same time each morning. New birds were reduced 10-12% in weight during training, so that they would respond readily to the test system but remain healthy. Lean venison was fed in daily amounts (about 15-20 grams) such that birds neither gained nor lost more than 2-3 grams during the test period. Ground multiple vitamins were added regularly, and when a bird dropped as much as 5 grams in weight beyond the initial 10-12% decrease, live mice were fed as a supplement.

In the holding room, birds were on a 12-hour light schedule. Two 300-watt ceiling-mounted bulbs illuminated the test room. Although temperature controls kept temperatures near 22 C in winter, temperatures occasionally reached 34 C in summer.

Daily training and testing sequence included weighing a bird, releasing it into the test room, and allowing 10 capture attempts with a particular test arrangement. A trial consisted of engaging the mercury switch so the motorized drum pulled the prey across the capture surface between the two tunnels. A reward of about 0.2 g venison was attached to the prey for each trial, so birds could receive up to 2 g of meat as a reward. A capture attempt included a test bird leaving the perch and attempting to catch the moving prey with its talons. Success was recorded when the test bird struck or grasped the prey before it reached the second paper tunnel. Linear distance in cm travelled by the prey from emergence to point of capture was recorded for each success, whereas a miss was recorded as a zero. Measurements of response to prey-capture opportunities were:

1) frequency of attempts in the first five trials;

2) frequency of success in attempts made during the first five trials; and

3) linear distance to capture for successes in the first five trials.

The first five trials were used because birds seemed to respond uniformly up to five, but were more erratic thereafter. When measures of physical ability to make captures, rather than response, were desired, frequency of capture and mean distance to capture for first five actual attempts were used.

Three experimental treatments and one combination of two treatments were used:

1) Exposure Distance - that distance between tunnels in which a kestrel could capture prey. It was varied in 10 cm intervals between 110-60 cm.

2) Prey Contrast - that difference in light reflectance between prey models and black background. Prey model covers of 18, 15, 12, 9, and 6% reflectance were used on 6% black capture surface.

3) Cover Density - that amount of the path of the prey between tunnels which was obscured by black paper tunnels with cutout strips. Densities of 20-90% were used in 10% intervals.

4) Cover-Contrast Combination - 60% cover was combined with prey models of 15, 12, 9, and 6% reflectance.

Prey speed was 62 cm/second for all tests, and in all except Exposure Distance tests 120 cm was used as maximum linear distance between tunnels. Prey reflectance in Exposure Distance and Cover Density tests was 20%.

Two groups of test birds were used. In July of 1968, three downy young kestrels, one female and two males, were obtained from a nest. From early January through May 1969, 12 wild kestrels (8 males and 4 females) were trapped, trained, and run through the experimental design described below. Aging by plumage was not reliable for the 12 wild-trapped birds, so they were considered as a group of sub-adults and adults.

In the first group, three kestrels were obtained at about four weeks of age, were reared by hand and, beginning one week after fledging, were trained as previously described, and tested for development of prey-catching ability. All of their prey-capturing experience was in this experimental system. Exposure Distance, Cover Density, Prey Contrast, and Cover-Contrast Combination tests were run in order. Birds were tested by starting at minimum difficulty levels and increasing at one-step intervals daily to a maximum performance level.

In the second group, 12 wild-trapped kestrels were randomly assigned in groups of 4 for testing at one of 3 treatment groups within Initial Response and Learning

Rate tests for each of the 3 Experimental Treatments (Figure 2). The 12 kestrels were randomly reassigned to groups 6 times during testing, twice for each Experimental Treatment. In the Initial Response tests, groups of four birds were tested at totally new treatment levels for Exposure Distance, Prey Contrast, and Cover Density. In Learning Rate tests groups of four birds were tested at three different daily rates of change in treatment for Exposure Distance, Prey Contrast, and Cover Density. Birds that ceased to perform at advanced daily rates of change were returned to a previously successful level and offered one-step daily rates of change in treatment until a Maximum Performance level was reached. This sequence was used within treatments for Exposure Distance, Prey Contrast, and Cover Density, in order, and a Cover-Contrast Combination test was then run. Testing took about 30 days (Figure 2).

TEST SEQUENCE →

EXPERIMENTAL TREATMENTS	INITIAL RESPONSE	LEARNING RATE	MAXIMUM PERFORMANCE
I EXPOSURE DISTANCE	4 birds assigned to each distance group: 100, 80, and 60 cm	4 birds assigned to each decrease rate: 10, 20, and 30 cm/day	Each bird carried to minimum distance
II PREY CONTRAST	4 birds assigned to each reflectance group: 18, 12, and 6%	4 birds assigned to each decrease rate: 3, 6, and 9%/day	Each bird carried to minimum contrast
III COVER DENSITY	4 birds assigned to each density group: 20, 40, and 60%	4 birds assigned to each increase rate: 10, 20, and 30%/day	Each bird carried to maximum density

Figure 2. Testing sequence for 12 kestrels randomly assigned to groups in Initial Response and then Learning Rate for each experimental treatment. Sequence requires about 30 days.

RESULTS

Field Data

Fifty-four prey capture attempts by 20 kestrels were observed in Clinton, Ingham, and Shiawassee Counties, Michigan from June 1968 through June 1969. Half of these observations were made during April, May, and June, 1969. In a capture attempt identifiable features were: time of day, method of hunting, habitat being hunted, weather, and (not always) whether or not prey was captured. Captured prey could usually be identified, but in an unsuccessful attempt the prey, its activity, and exact position in the habitat were unknown. Because of this, identification of specific influences on prey capture success was difficult.

Sex and age of hunting kestrels were not easily determined because of light direction and rapid movements by the birds. Kestrels were frequently observed hunting earlier (before 7:00 a.m.) and later (after 7:00 p.m.) than reported in natural history studies (Bent 1938), but since I did not trap at all times of day I have no quantitative data on temporal characteristics of hunting. During heavy or prolonged rain or snow, or strong winds, kestrels stopped hunting and perched under cover. During a break in a storm or after it stopped they greatly increased their hunting activity.

Kestrels captured 17 prey items in 47 attempts from perches, and 1 prey item in 7 attempts by hovering for 33% success overall. The ratio of hovering to perching as a hunting method probably depended on abundance of perches overlooking productive hunting areas. Prey caught were 7 mice, 10 insects, and 1 snake. Hunting success was similar in crop and old field habitat, but kestrels hunted more than twice as often and caught correspondingly more prey in old fields (Figure 3).

Hand-reared Kestrels

Three hand-reared, totally inexperienced kestrels were tested in Exposure Distance, Cover Density, and Prey Contrast tests to follow development of their prey-capturing ability. These birds began capturing in the experimental system during training, about one week after fledging, and were soon highly conditioned to it. They anticipated the appearance of the prey model by leaning forward on the perch and staring intently, obviously ready to attack. Birds were started at 110 cm exposure distance, 18% prey reflectance, and 20% cover, and were run through tests at one-step daily intervals. Birds attempted 94%, 97%, and 80% of possible trials during testing, with no tries occurring haphazardly. Success in capturing prey dropped to 12/15 (80%) at 70 cm duration of prey exposure, and to 11/15

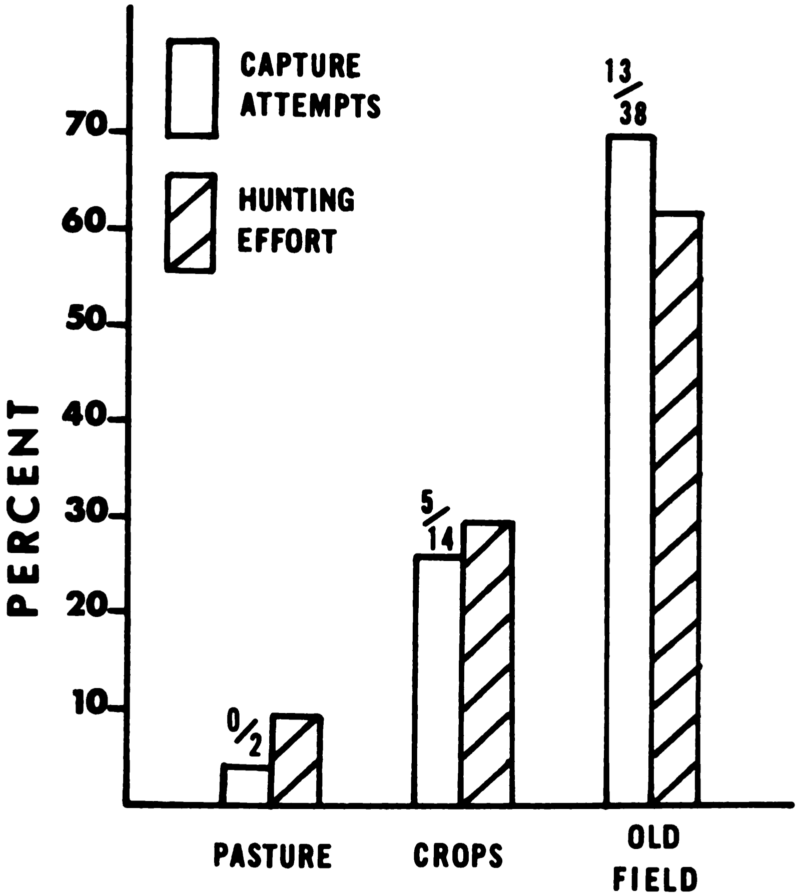

Figure 3. Comparison of hunting effort and prey capture attempts by habitat type for wild kestrels. At least 30 different birds were observed in 109 hunting efforts, and 20 of these caught 18 prey items in 54 attempts. Ratios over bars on graph indicate capture successes.

(73%) when there was 80% cover, but remained 100% throughout changes in prey reflectance (Figure 4). Mean distance to capture increased at 90% cover density. In prey contrast tests, mean distance to capture increased with a decrease in contrast for one kestrel but remained essentially the same for the other two.

Wild-trapped Kestrels

Training

Between days 2-4 during training mean distance to capture decreased almost 12 cm, then did not range more than from 105 to 110 cm through day 10 (Figure 5). Variation about the means was similar throughout the training period suggesting that the response of the 12 birds to the test system was comparable.

Initial Response

In Initial Response tests varying treatment levels were presented to kestrels never before exposed to manipulations of the experimental system. As duration of prey exposure to kestrel became shorter and contrast became less there were significantly fewer ($P < 0.05$) capture attempts (Table 1). There were significantly fewer ($P < 0.05$) attempts at 40 and 60% densities of cover than at 20% cover. Except for 80 cm in Exposure Distance and 60% in Cover Density, birds were 90-100% successful when they attempted captures. Observed differences in mean

Figure 4. Success in Exposure Distance treatments and success and mean distance to capture in Cover Density and Prey Contrast treatments for three hand-reared kestrels. Data represent five capture attempts per bird per treatment level, and number of successes appear over bars on graph.

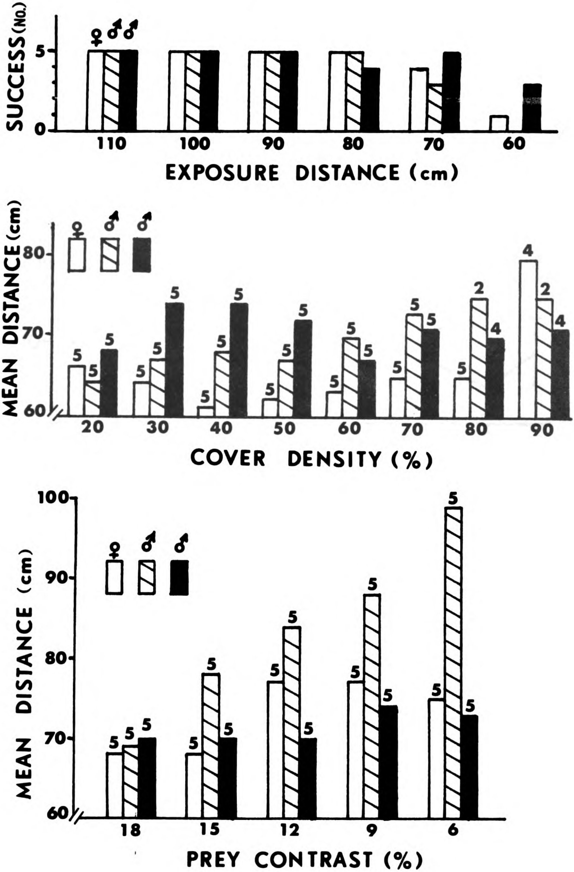
SUCCESS (NO.)
EXPOSURE DISTANCE (cm)
MEAN DISTANCE (cm)
COVER DENSITY (%)
MEAN DISTANCE (cm)
PREY CONTRAST (%)

Figure 4

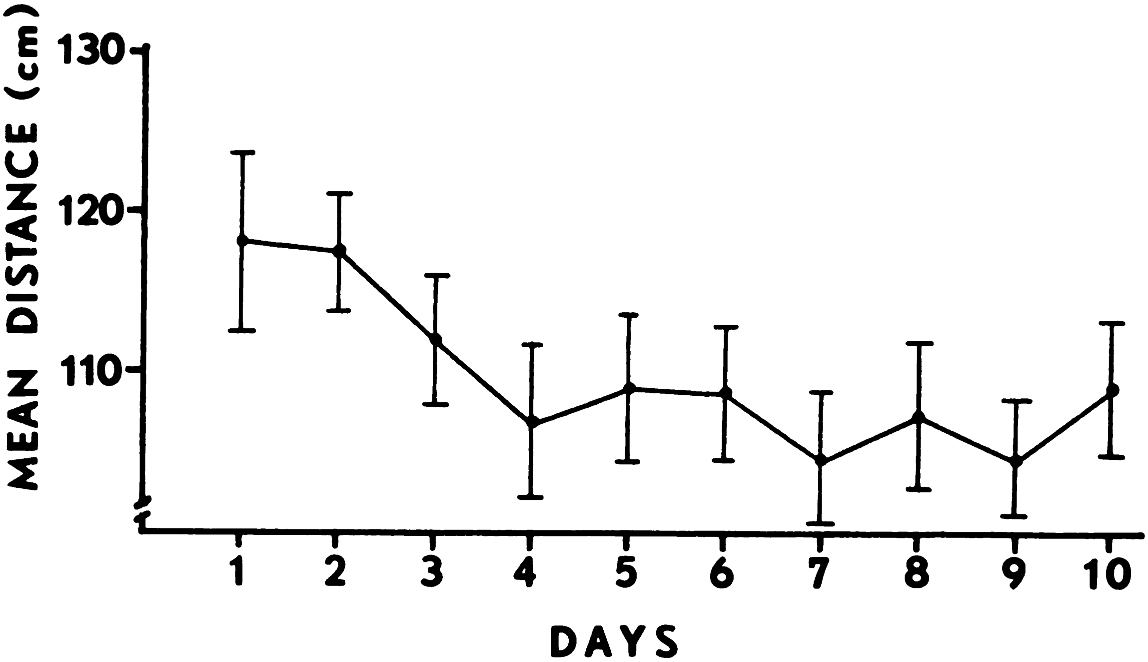

Figure 5. Mean distance to capture ($\bar{x} \pm$ S.E.) during training for 12 kestrels. Each point represents an average of daily means.

Table 1. Response to 3 experimental treatments in Initial Response tests by 12 kestrels arranged in groups of 4 per treatment category. Data represent first five trials per bird per treatment level.

Treatment	Birds that Tried	% Attempts	% Success	Mean Distance to Capture (cm) ($\bar{x} \pm$ S.E.)
Exposure Distance (cm)				
100	4	100	90	-
80	3	70	0	-
60	0	0 *	0	-
Prey Contrast (%)				
18	4	100	100	101 ± 2
12	4	85	100	98 ± 3
6	3	30 *	100	108 ± 5
Cover Density (%)				
20	4	100	100	89 ± 3
40	4	75	100	90 ± 2
60	4	65 *	62	94 ± 5

* X^2 significant at $P < 0.05$ using 2 x 3 contingency tables.

distance to capture were not significantly different due to high variability.

Learning Rate

Learning Rate data were analyzed by pooling number of attempts, number of successes, and mean distance to capture data, respectively, within each rate of change in daily treatment. Data were pooled to represent an overall performance of a group of four birds at a given rate of change in treatment. Data were pooled within one- and two-step (e.g. 10 and 20 cm increments in Exposure Distance) rates of change where both groups performed at the same treatment levels, and compared, and data were similarly pooled and compared for one- and three-step (e.g. 10 and 30 cm increments in Exposure Distance) rates of change. These tests were run to determine the rate at which kestrels adapt to shortened duration of prey exposure, reduced contrast of prey to substrate, and greater cover density.

There were significantly fewer ($P < 0.05$) capture attempts by kestrels in 20 cm or 30 cm decrease groups than by the 10 cm decrease group in Exposure Distance (Table 2). The 30 cm group was significantly less ($P < 0.05$) successful than the 10 cm group. In Prey Contrast tests the 6% decrease group attempted significantly fewer captures than the 3% group ($P < 0.05$) but there was no difference in attempts between 3% and 9% groups. Success was 100%

Table 2. Comparison of responses to three experimental treatments in Learning Rate tests.[1] Twelve kestrels arranged in groups of four per treatment level. Data represent first five trials per bird per day.

Comparison of Daily Rates of Change in Treatment	No. of Levels of Comparison	% Attempts		% Success		Mean Distance to Capture (cm) ($\bar{x} \pm$ S.E.)	
Exposure Distance (cm)							
10 with 20	3	95	77 *	61	62	-	-
10 with 30	2	92	75 *	81	60 *	-	-
Prey Contrast (%)							
3 with 6	3	95	68 *	100	100	98 ± 2	99 ± 1
3 with 9	2	87	80	100	100	98 ± 2	95 ± 2
Cover Density (%)							
10 with 20	4	81	82	90	98	89 ± 1	96 ± 1
10 with 30	3	78	73	87	93	87 ± 1	95 ± 2

* X^2 significant at $P < 0.05$ using 2 x 2 contingency tables.

[1] Where one- and two-step or one- and three-step groups performed at the same treatment levels, data were pooled within groups and compared for differences in response.

for both 3% and 6%, and 3% and 9% comparisons. Two male kestrels contributed the reduced number of attempts at 6%. Part of this variation may have been refusal to respond to the experimental system rather than direct effects of experimental treatments. Mean distances to capture were unaffected by rate of change in Prey Contrast. There were no significant differences in attempts or successes between rate groups in Cover Density, but both 20% and 30% groups had higher mean distances to capture. Birds were successful when they tried to catch prey, whether at one, two, or three-step daily rates of change in Prey Contrast and Cover Density.

Cover-Contrast

In Cover-Contrast tests 60% cover was combined with 15, 12, 9, and 6% prey reflectance to assess the effects of two experimental treatments on prey-catching ability. Capture attempts and successes decreased significantly ($P < 0.001$) with reduced contrast in the 60% cover combination (Table 3). Birds were successful when they tried with no cover, but tried less and caught less with cover. Mean distances to capture were greater with 60% cover than with no cover at 9% and 6% prey reflectance, with greater variability at 6% probably due to a small number of captures. Overall performance dropped most clearly at 6 and 9% reflectance - which is logical since these levels combine low contrast with heavy cover.

Table 3. Response to Cover-Contrast tests by 10 kestrels compared to performance of 4-12 kestrels[1] in Prey Contrast tests without cover. Data represent first five trials per bird at each reflectance level.

Percent Reflectance	% Attempts		% Success		Mean Distance to Capture (cm) ($\bar{x} \pm$ S.E.)	
	No Cover	60% Cover	No Cover	60% Cover	No Cover	60% Cover
15	80	72	100	100	96 ± 3	88 ± 1
12	87	65	100	90	96 ± 2	95 ± 2
9	75	56	75	60	97 ± 2	103 ± 2
6	68	46 *	100	30 *	99 ± 2	102 ± 4

* X^2 significant at $P < 0.001$ using 4 x 4 contingency tables.

1 For No Cover, data are included for 4 birds at 15%, 8 birds at 12 and 9%, and 12 birds at 6%.

Maximum Performance

Maximum performances for 12 kestrels used in the experimental design are presented in Table 4. In all cases during testing, birds which stopped performing at some level during Learning Rate tests were carried to higher performance levels by dropping back to a previously successful treatment level and proceeding at one-step intervals. In Prey Contrast tests all birds except one caught black prey on a black background with 95% overall success, but in Exposure Distance and Cover Density tests birds varied more in performance.

Comparison of maximum performances of the 12 wild-trapped birds (Table 4) with performances of three hand-reared kestrels (Figure 4) shows that hand-reared birds performed much better than the average for wild-trapped birds in Exposure Distance, Cover Density, and Prey Contrast experimental treatments. Success rates were similar but mean distances to capture were consistently lower for hand-reared kestrels (Figure 4).

Table 4. Maximum Performance by 12 kestrels in Exposure Distance, Prey Contrast, and Cover Density treatments. Data represent five capture attempts per bird.

Treatment	No. Birds	% Success	Mean Distance to Capture (cm) ($\bar{x}$ ± S.E.)
Exposure Distance (cm)			
90	1	100	-
80	8	50	-
70	2	80	-
60	1	70	-
Prey Contrast (%)			
9	1	-	-
6	11	95	102 ± 3
Cover Density (%)			
70	3	80	100 ± 6
80	6	83	98 ± 4
90	3	40	93 ± 5

DISCUSSION

Responses to Prey

Kestrels are basically ground-oriented in seeking prey, and, even though they often concentrate on field mice or grasshoppers, they will take as prey reptiles, a variety of insects, small mammals, and a few birds. A very strong orientation to one specific prey item would be a disadvantage if that prey item suddenly became unavailable. It would be advantageous for a kestrel to be able to respond to a wide range of prey items which appear in a similar way. Grasshoppers, mice, reptiles, and many small birds move along the ground, in and out of vegetation, and essentially offer similar prey-capture opportunities. In experiments in this study, the prey model was always the same size and shape and moved at a constant rate, so differences in response by kestrels to the prey model were presumably due to variations in duration of exposure, prey contrast to substrate, or density of cover.

Factors Affecting Prey Captures

Prey-catching success in raptors may be affected by the following:

1) characteristics of the raptor - age (experience), sex, physiology (related to breeding), hunger state, individual variation in physical ability, genetic stock;

2) environmental factors - weather, light intensity, substratum (vegetation and terrain); and

3) characteristics of the prey - prey type (bird, mammal, etc.), age, size, coloration, habits, type of prey movement (sedentary or mobile).

Experience was chosen as the most likely characteristic of the raptor to affect prey capture success since every individual is exposed to different combinations of environmental situations in which it must capture prey. Density of cover was chosen as a potentially important environmental factor since catching prey would seem more difficult when cover is heavier. In these experiments, prey configuration and movement were fixed to resemble field mice, and prey contrast to substrate was chosen as an important combination of prey characteristics and environment since concealing coloration or shading are often developed by prey to help escape predators. The above mentioned variables were chosen for use as experimental treatments in this study because they are biologically important and can be manipulated experimentally. Response of kestrels to tests which vary duration of prey exposure, contrast of prey to background, and density of cover, are used here to describe perceptive and physical characteristics of prey-capture in kestrels.

Responses to Prey Capture Opportunities

In the experimental system, kestrels responded to a prey-capture opportunity in this sequence:

1) visual detection of and orientation to the moving prey model;

2) a period for responding to stimuli from the prey-catching opportunity;

3) an attack or not based on the response period;

4) if an attack was initiated, there followed either an attempt to grasp the prey model or cessation of the attack in flight.

If a favorable stimulus persisted long enough when the opportunity was first perceived, an attack was started. If the favorable stimulus did not persist during flight the attack was ended. In this test system kestrels responded to an opportunity in sequence and were successful or not within about 0.9 - 1.8 seconds. In the situation which demanded the quickest response to ensure success, 60 cm duration of prey exposure, kestrels took about 0.10 seconds to start their attack. With longer duration of prey exposure kestrels took longer to launch an attack. The second response period - in flight - was not measurable but the strength of the stimulus could change gradually as the prospects for success diminish during the attack.

Some minimum duration of prey vulnerability may provide a stimulus threshold, which must be reached to induce an attack, and maintained to ensure its completion.

The importance of variation in length of response periods when kestrels were sizing up capture opportunities was not fully recognized during testing, so only infrequent measurements were made. Much longer response periods were taken by birds during training than during subsequent testing. At the training distance of 160 cm between tunnels, prey models were allowed to travel as far as 80-100 cm, or for more than one full second, before capture attempts were begun. Kestrels used in the experimental design captured at a mean distance of above 105 cm during training, but when entered first in the testing sequence into Exposure Distance tests, eight attempted captures and were 50% successful at 80 cm. This means that when a capture situation demanded it, a kestrel could respond and attack or not in much less time (down to 0.10 second) than during training. After Exposure Distance trials eight birds continued to capture at distances shorter than those in training, three remained the same, and one performed at slightly larger distances. Apparently kestrels learned to respond more quickly during Exposure Distance trials, and continued to do so thereafter.

Wild kestrels started capture attempts by searching a field visually from a perch, orienting to prey below by staring intently and bobbing their heads (apparently to focus on the prey), then they began an attack but frequently pulled back before reaching the ground. The sequence of responses described earlier may be applied to capture attempts in the wild. The in-flight response period probably affects capture attempts more often in the wild since they occur at greater distances than in my experiments, thus providing more time for an opportunity to deteriorate in its prospects for success.

An important factor in successful prey capture not measured directly in these experiments was the ability of kestrels to grasp and hold prey. Differences between birds were noted during training, but were not measured because it was difficult to see details of the swift foot movements. Some birds struck the capture surface with both feet and then snatched the prey with one foot, others struck the prey with both feet. Some would not hold the prey against the pull of the motor, whereas others pinned the prey aggressively and held it firmly. It seemed that several birds struck at the prey harder with cover strips present than without, and it is possible that certain potential obstructions to success might provoke increased intensity of effort by an attacking kestrel. Increased effort in the form of aggressive grasping and holding, or striking at the prey very hard, would seem to be an advantage in catching quick-moving Microtus which may often weigh half as much as the kestrel.

Effects of Experience

Learning to recognize some combination of stimuli, or a total image of a prey-catching opportunity may enable kestrels to decide whether to attack or not. Initial Response tests (Table 1) show that birds inexperienced in each experimental treatment were cautious about making attempts when success was in doubt (fewer attempts at short exposure distance and low contrast). After gaining experience, kestrels attempted captures and were successful in treatment levels at which inexperienced birds would not try (Table 4). It appears that ability to recognize a promising prey-capture opportunity develops with experience. Learning Rate tests suggest that kestrels can adapt to rapid changes in prey contrast and cover density, but cannot adapt to rapid reduction of duration of prey exposure (Table 2).

Survival Significance

If no danger or expenditure of energy were involved in a prey capture, a kestrel could afford to respond indiscriminately to anything that looked like prey - simply grabbing whatever turned out to be useful, or flying away when the prey was of no food value. The three hand-reared birds used in this study reacted to the prey model without hesitation. They were highly conditioned to the test system and by-passed any delay in the initial response period in making capture attempts. They reacted "automatically" to prey movement and attacked in situations wherein no wild-trapped kestrels would make attempts. These birds associated prey capture with food only, having had no bad or unsuccessful experiences to make them look over the situation before attacking. In contrast, wild-trapped birds "looked over" each prey-capture opportunity before attacking in experimental prey-captures. It would seem to be an advantage to be able to evaluate the total opportunity before attacking, both to avoid waste of energy and potential physical danger. This ability was exhibited by wild-trapped birds which had apparently learned in the wild that it was to their advantage to respond to some opportunities but not to others.

Little is known about the survival of young raptors of all species after fledging, and mortalities are assumed to be high during the first fall and winter (Beebe and Webster 1964). Young raptors have trouble getting enough food (Errington 1967:35), and it is likely that inexperienced birds would not adjust easily to finding food in totally new environments during migration. The three hand-reared kestrels used in this study performed consistently better on a physical basis (mean distances to capture were shorter) than did wild-trapped birds. Part of the difference is due to hand-reared birds being highly conditioned to the system and responding quickly to the prey model. I interpret these data to indicate that young (inexperienced) and adult (experienced) kestrels differ little in physical ability to capture prey once an attack is started. Differences in abilities to judge prey-capture opportunities - greater ability being gained through experience - may affect survival in kestrels. Such differences might be magnified in unfamiliar environments - as are encountered when young leave the nesting area or migrate.

Success in catching prey is important to predators in maintaining a balance of energy output and intake (Emlen 1968). In periods of physiological stress - as in cold winters in Michigan, or during migration - efficiency in capturing prey would be of survival significance. I have insufficient data to present success rates by seasons, but the 33% success noted for kestrels in Michigan may be compared with 7% success recorded in Sweden for four species of raptors (Rudebeck 1950). Kestrels catching mice and insects in familiar territory in Michigan are obviously under more favorable conditions than migrating raptors attacking mainly avian prey. Perhaps the low success rate reported by Rudebeck was compensated for by an abundant supply of migrating birds as a prey source which ensured frequent capture opportunities. In experiments done in this study, especially in Initial Response tests (Table 1), kestrels were usually successful when they attempted captures. This emphasizes the importance of proficiency in responding only to promising capture opportunities, and thus avoiding wasted effort.

Effects of Experimental Variables

Every prey-capture opportunity, in the wild or in the laboratory, is affected by duration of prey exposure either during the response period when the stimulus to attack or not is received, or during the attack when physical limitations of flight speed demand some minimum duration of prey exposure for the kestrel to reach the prey. Even though the 120 cm distance used in Prey Contrast and Cover Density tests was not near physical limits for the birds, they still had to respond and attack quickly to catch prey, influenced by differences in contrast and cover. Duration of prey exposure affected number of attempts and success more than prey contrast or cover density throughout testing, and may be the most important factor affecting capture success when kestrels are pursuing highly mobile prey like field mice.

Variations in contrast of prey to substrate affected responses of test birds significantly in Initial Response tests (Table 1), with most birds responding similarly to contrast changes throughout other tests (Table 4). Apparently kestrels in this study could detect movement alone or see shadows under the prey model, since they efficiently captured a black prey on a black background. Prey models were covered with a coarse cloth which had "facets" that reflected some light and may have aided kestrels in seeing the prey model. In the wild, texture of prey skin or pelage, and of soil or vegetation may influence light reflectance and thus conspicuousness of prey. Concealing coloration of prey has been shown to aid the prey in escaping predators (e.g. Dice 1945). While responses to prey were not affected much by variations in contrast in this study, mean distances to capture were larger in Prey Contrast tests than in Cover Density tests (Tables 1 and 2). These differences may indicate that low contrast resulted in longer response periods before an attack was made.

Similar subtle effects of variations in cover density appear in fewer attempts (Table 2) and larger mean distances to capture (Tables 1 and 2) when cover is dense. Perhaps prey contrast and cover density affect prey captures only at very low contrast and very dense cover,and these effects appear only as slight differences in performance.

Combinations of potential inhibiting influences on prey-capture success should affect success more than single influences. Combination of 60% cover density with 15, 12, 9, and 6% prey reflectance resulted in reduced response in terms of fewer attempts, less success, and increased mean distances to capture at 9% and 6% reflectance (Table 3). Neither prey contrast nor cover density alone affected prey capture much after initial responses, but in combination significant differences appeared. In the wild, combinations of cover density, prey contrast, and other factors could affect prey captures in many ways. A conspicuous prey crossing a grassy spot might stimulate a kestrel to start an attack, but if the prey suddenly moved into denser cover or a different colored or shaded background the kestrel might lose sight of it and cease the attack in progress. I have seen kestrels start attacks at a flying grasshopper but lose sight of it as it landed on a substrate which offered concealment, then either fly off or land nearby and search visually for the insect. Similar encounters with all prey types are undoubtedly affected by combinations of environmental factors and prey characteristics.

Within limits similar to those described in this study, wild kestrels can effectively capture prey in dense cover, and can effectively capture prey of little contrast to the substrate. When these influences are combined - undoubtedly with other environmental factors - inhibition of prey-capture success may occur. Environmental influences or prey characteristics simply control the relative amount of exposure of the prey to the kestrel by obscuring it or making it less conspicuous. The most important variable studied here was duration of exposure of prey to kestrel - a variable which influences responses to every prey-capture opportunity. Regardless of other influences on a prey-capture attempt, kestrels are physically limited in their ability to perceive prey and attack quickly. The length of time prey is exposed to the kestrel controls whether or not an attack is started, whether it is carried through, and ultimately whether a capture is made.

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