CHICAGO JOURNALS

The University of Chicago

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Author(s): Leonard F. Ruggiero, Carl D. Cheney and Frederick F. Knowlton

Source: *The American Naturalist*, Vol. 113, No. 5 (May, 1979), pp. 749-757

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2459965>

Accessed: 16/12/2014 12:55

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INTERACTING PREY CHARACTERISTIC EFFECTS ON
KESTREL PREDATORY BEHAVIOR

LEONARD F. RUGGIERO,* CARL D. CHENEY, AND FREDERICK F. KNOWLTON

Department of Wildlife Science and Department of Psychology,
Utah State University, Logan, Utah 84322

Many factors have been named critical variables controlling the reactions of predators to prey. Prey movement, suggested by Cushing (1939) and Ingles (1940), has been shown to be involved in predation by owls (Metzgar 1967; Kaufman 1974), kestrels (*Falco sparverius*) (Sparrowe 1972), red-tailed hawk (*Buteo jamaicensis*) (Snyder 1975) and ferruginous hawk (*B. regalis*) (Snyder et al. 1976). Mueller (1971, 1972, 1975) has proposed prey "oddity" as another crucial variable in kestrel predatory behavior. He further suggests (Mueller 1974) that raptors respond positively to "novelty" and that novel prey are selected by raptors in nature. Coppinger (1969, 1970) has demonstrated that novel (unfamiliar) food items are rejected by some avian predators and Rabinowitch (1968) has shown similar avoidance of novel food by gull chicks.

Novelty and *oddity* are terms requiring operational definitions. We contend that a great deal of confusion results from nonoperational use of these and similar terms (i.e., conspicuousness, search image). Furthermore, the influence of experience (learning) by predators is seldom adequately managed in experimental studies. Prey novelty, by definition, must decrease as a function of repeated exposure of prey to the predator. A stimulus can only be novel once. In studies with repeated trials total novelty as unfamiliarity must dissipate (Menzel 1963).

It may be that studies which manipulate only one variable at a time have contributed about all they can. It is now possible to utilize the data from such studies in designing and conducting more complex and relevant experiments in which interactions are observed. This report considers predator experience, prey movement, color, and morphology all to be relevant variables and was designed to analyze their interactions as they influenced American kestrel prey selection.

METHOD

Two male and two female adult American kestrels (*Falco sparverius*) were wild-caught and immediately free-lofted in individual aviaries. Within 2 days they were conditioned to fly to a perch and feed on a skinned mouse as the handler left the enclosure. No attempt was made to tame the birds. Experimental trials began on the third day of captivity.

* Present address: U.S. Department of Agriculture, Forest Service, Bighorn National Forest, Sheridan, Wyoming 82801.

TABLE 1

INDEPENDENT VARIABLES AND CORRESPONDING TREATMENTS FOR PREY CHARACTERISTICS

Prey Variables	Characteristic	Treatment
Movement*	No movement	Dead mouse
	Aberrant movement	Mouse injected with .01 cc/6 g body wt 25 % sodium pentobarbital.
	Normal movement	Untreated
Pelage color*	White	White pelaged mouse
	Black	Black pelaged mouse
Morphology	Familiar morph	Normal mouse without treatment or modification
	Unfamiliar morph (smaller mice were used in this category to equate overall apparent size)	A mouse with a 7.5 cm piece of black or white yarn tied to its tail and a 1.2 cm black or white cotton ball affixed to its back.

* Based on the 66 mice in experiment 1, the quantity of movement for aberrant and normal mice was not significantly different ($P = .05$, $\chi^2 = 1.54$), nor was black vs. white ($P = .05$, $\chi^2 = 0.34$).

All aviaries were $6 \times 3 \times 3$ m and were covered with 1.3 cm^2 wire mesh. Posts ($10 \times 10 \text{ cm}$) 1.9 m high served as perches and were each positioned vertically along the midline of the enclosure 1.5 m from the north walls. Aviary substrates consisted of 10 cm of dark brown peat moss.

A pair of mice (*Mus musculus*) were presented by the experimenter; dead mice were semirandomly positioned in a lifelike posture within the arena. (Dead prey were never placed where an immediately previous "kill" had been made.) As the experimenter left the aviary the bird was allowed to select one prey item during a 15-min trial. A trial in which no selection was made was recorded as such. Since two unacceptable prey items could be presented in the same trial, requiring kestrels to select one would not reflect the bird's normal response. Furthermore, the experience gained from such a constrained trial might modify subsequent responses; hence, following a no-choice trial the kestrel was fed a skinned dead mouse. Thus, no pelage color association was made and the bird's deprivation level was held relatively constant. Data collected on each trial included time from prey release to kill, amount of prey movement, item selected, and prey position at time of attack.

The independent variables (prey characteristics) were divided into treatments as defined in table 1. One treatment for each of the three variables was used for each prey item, thus defining 12 distinct prey types. For example, one type was a black, familiar, normally moving mouse (item 11, table 2).

The research design was a $2 \times 2 \times 3$ factorial with 66 trials for all possible prey item comparisons. The design was balanced and χ^2 analysis used to assess main effect and interaction relationships (Cochran and Cox 1950, p. 103). (References to "interaction analysis" and "main-effect" analysis are indicated when interactions of the response to a combination of variables are not commensurate with responses to the same variables independently. The degree of synergism resulting from combina-

TABLE 2

PREY ITEMS AND THEIR ASSOCIATED CHARACTERISTICS SHOWN ON A PER TRIAL BASIS INCLUDING
RELATIVE PROBABILITIES OF SELECTION

ITEM No.	CHARACTERISTICS*	ITEM No.											
		1	2	3	4	5	6	7	8	9	10	11	12
1	A. M., W., U.												
2	Norm. M., W., U.	1											
3	No M., W., U.	3	3										
4	A. M., B., U.	4	4	3									
5	Norm. M., B., U.	5	n.t.	3	n.t.								
6	No M., B., U.	6	6	6	6	6							
7	A. M., W., F.	7	n.t.	7	7	7	6						
8	Norm. M., W., F.	8	2	3	n.t.	n.t.	8	7					
9	No M., W., F.	9	9	3	4	n.t.	6	9	8				
10	A. M., B., F.	10	10	10	10	5	10	10	10	10			
11	Norm. M., B., F.	11	11	3	11	11	11	7	11	11	10		
12	No M., B., F.	12	12	12	12	12	6	12	8	12	10	11	

NOTE.—Numbers within table body designate the selected prey item of the pair offered on each trial; n.t. indicates no selection.

* Prey characteristics—A. M. = aberrant movement; Norm. M. = normal movement; No M. = no movement; W. = white; B. = Black; U. = unfamiliar; F. = familiar.

tions of variables determines the significance of a particular interaction. Main effect analysis disregards potential interactions and points out the response to a variable over all combinations with other variables. Thus, the result of main effect analysis could be a choice which in reality is a function of an interaction. Therefore, main effect analysis is potentially misleading, depending on the presence or absence of appropriate interactions.)

Statistical consultation suggested χ^2 as a robust test, less sensitive to traditional constraints in this instance. (The assumption that row and column totals are completely unrestricted is not satisfied.) It is important that test results do show agreement, and data and statements regarding significance should be viewed in this context.

The design was accommodated by using each of the four kestrels in a series of trials (sets of 16, 16, 17, and 17 trials). Within practical limits, this procedure minimized the influence of learning, which would be profound if fewer birds or more trials were used. The zeta technique (Kendall 1948) was used to calculate the coefficient of selection consistence. Zeta falls within the range of 0–1 with zero indicating inconsistent selection. The χ^2 statistic was subsequently used to test the hypothesis that zeta resulted from random choice as opposed to a nonrandom preference scheme.

RESULTS

Selection biases were not apparent for prey location or relative predator-prey proximity at time of attack. Kestrels selected the relatively closer mouse 36% of the time while selecting the relatively farther mouse 28% of the time. Mice were equidistant from the kestrels in 36% of the selections.

Selection data were put into a form which facilitated the examination of each

FIG. 1.—Selection probabilities of morphology and color contrasted across the movement variable.

experimental trial (table 2). The numbers within the body of table 2 indicate which of the pair was selected. The description for each item is provided. Relative preference probabilities were calculated for each prey item on the basis of observed/possible selection. The relationship between variables and the influence of interactions upon these relationships is illustrated in figure 1. A significant interaction was found between movement and morphology, suggesting that the levels (treatments) of these variables did not act independently to produce the observed results ($P = .01$; $\chi^2 = 15.042$). Unfamiliar moving morphs were selected on less than 20% of the opportunities. However, selection for the unfamiliar morph increased to 68% when combined with no movement. Familiar morphs were selected at the rate of 73%, 53%, and 46% when combined with aberrant movement, normal movement, and no movement, respectively. Hence, selection was very high for aberrantly moving familiar mice, but very low for unfamiliar mice showing any movement.

Other variable combinations (i.e., pelage color-morphology and pelage color-movement) did not interact significantly. Therefore, selection for morphology and pelage color variables is reasonably reflected in main-effect analysis. Main-effect selection within morphology (unfamiliar vs. familiar) and pelage color (white vs. black) variables indicates preference for familiar morphs and black color. These differences were found to be significant ($P = .01$; $\chi^2 = 7.842$) for both within variable tests.

Six trials resulted in no selection, i.e., "ties." These ties were broken in all possible ways for calculation of zeta, the coefficient of consistence. The highest value of zeta thus obtained was .64; therefore, selection was reasonably consistent. The hypothesis that selection was the product of random choice was then tested using χ^2 . For

purposes of this test the lowest value of zeta was used, i.e., ties were broken such that inconsistency was maximized. Results indicated that selection was a function of a nonrandom scheme ($P = .005$; $\chi^2 = 15$). Theoretically, this preference scheme might represent the amalgamation of four different nonrandom preference schemes. Subsequent results showed this not to be the case.

Experiment 2.—Relative selection probabilities were calculated from the data in table 2. These probabilities were then arranged to form a prey selection preference scheme. This was construed as a model of selection preference which could be compared against independent data. That is, if selection preferences by different individual kestrels were predicted by this model, it could be argued that such a preference scheme accurately reflects kestrel predatory preferences in this experimental situation. The results of such a comparison support the findings of the first experiment, and a brief description of experiment 2 is given below.

Two naive kestrels (one male and one female) were used in 25 trials each for the purpose of gathering independent data to which the preference scheme could be applied. These two kestrels were allowed greater experimental experience via (1) a more lengthy single series of selections, (2) a 2-wk pre-experimental period when birds were offered only a black or a white live mouse on alternate days, and (3) birds were constrained to make a selection on each trial (or 60 min elapsed, in which case the trial was repeated the following day). Predator-prey proximity was allowed greater latitude by not restricting the mouse to part of the enclosure. These procedural modifications provided for the subsequent analysis of differential predator experience and relative prey proximity as they may also be shown to interact and to influence prey selection.

The two kestrels in experiment two made identical selections in 19 of the 25 trials with no significant between-bird difference in observed prey selection ($\chi^2 = 1.90$). The model generated from the first experiment accounted for 38 of 50 trials, or 76% of the selections. Furthermore, seven of 12 trials for which the preference scheme failed to account came late in the series, thus, we think, reflecting the experience differential of the birds used in the two experiments. By examining only the first 17 trials for each bird in experiment 2, 86% of the selections were accounted for by the preference scheme. This indicates to us the importance of experience in this kind of study. Novel (unfamiliar) or otherwise originally unacceptable stimuli became familiar with exposure, hence acceptable, and response probabilities changed accordingly. This transition gradually occurred as some function of exposure to different prey types, and therefore relative differences in acceptability decreased. No significant overall relationship existed between prey selection based on relative proximity and preference model accountability ($\chi^2 = .087$). However, in all experiment-2 trials where deviant selections were made after trial 17, the closer prey item was selected. The trend is clear and suggests that transition from one set of prey acceptance criteria to a different set can occur in a relatively short period as some function of learning.

DISCUSSION

This research investigated some variables known to affect prey selection in the wild. The results suggest that (1) kestrels are more likely to attack prey to which they

are accustomed (i.e., familiar, not novel), (2) significant interactions do occur between prey characteristics, and (3) movement decreases rather than increases selection for unfamiliar morphs. Unfamiliar morphology, white pelage, and no movement characteristics were selected significantly less than familiar morphology, black pelage, and movement. Results (1) and (2) seem consistent with what we would expect based on probable predator conditioning via their wild experience.

Movement as a prey-associated stimulus.—The results with regard to movement are consistent with the findings of others. Kestrels in the present studies preferred awkwardly moving (drugged) individuals when familiar (morph and color) prey were involved. Kaufman (1974) has shown differential predation for active versus inactive mice by barn owls (*Tyto alba*). Snyder (1975) showed active mouse prey selection with a red-tailed hawk in a paired prey choice situation. Snyder et al. (1976) also report increased selection for active prey by a ferruginous hawk. Eutermoser (1961), using trained peregrine falcons (*Falco peregrinus*), reported that 40 of 100 crows taken as prey were handicapped (aberrant movement?) in some way.

Cott (1940) has theorized that the attractiveness of abnormal prey movement may be an explanation for the evolution of distraction displays, alluding to active predatory selection of abnormally moving prey. Other researchers (e.g., Cushing 1939; Cade 1967; Errington 1967) have suggested that predators evaluate their chance for success when encountering prey and such evaluation involves active selection for abnormal movement, which is sometimes associated with injury or sickness. Mueller (1974, p. 718) points out that "... there are strong theoretical arguments for the selection of unfit prey and the concept has won wide acceptance from biologists." The present results are evidence that in fact kestrels do actively select abnormally moving prey.

Familiarity as a prey-associated stimulus.—The unacceptable quality of novel (unfamiliar) prey items, in our research, supports Coppinger (1969, 1970) and Rabinowitch (1968). Investigating the feeding behavior of blue jays and gull chicks respectively, these workers reported avoidance of various degrees of novelty, and an overall significant rejection of novel food items (neophobia).

As described by Menzel with chimpanzees (1963, p. 1): "The 'innate response' to a given stimulus object is a potential sequence of behavior patterns which, strictly speaking, is neither elicited by the stimulus nor emitted in vacuo by the subject; it is a product of a complex interaction in which the properties of the stimulus, the history of the subject, and present circumstances must all be taken into account." In the case of familiarity, it is clear that the interaction of stimulus characteristics, and subject (both predator and prey) history (experience), is of paramount importance (Mitchell 1973). That is, novelty (unfamiliarity) has some inverse relationship with experience, whereas "odd" or "not-matching" in the context of a sample set is not a sufficient condition to establish a novel stimulus property (Mueller 1975). Montgomery (1955) in primates found approach-avoidance conflict to be generated by novel stimuli as a function of the relationship between the exploratory and fear drives. Montgomery concluded that the strength of the fear drive evoked by novel stimulation decreases as the amount of experience (familiarity) with the stimulus increases. Conversely, lack of experience with a novel stimulus is a sufficient condition for eliciting fear and hence avoidance behavior (Mitchell 1973).

Movement as it interacts with familiarity.—Theoretical considerations as suggested by Coppinger (1970) are consistent with the above framework and are germane to a discussion of movement as it interacts with familiarity. The basic idea suggests that various stimuli have the potential to differentially arouse an animal, and the response to a given stimulus is a function of arousal level. A specific arousal level results from the interaction of physiological events, behavioral events, and an environmental stimulus. "Depending on the degree of novelty and the experience of the animal, some stimuli could actually increase the rate of attack by making the animal more alert, therefore behaviorally more efficient, or decrease the rate of attack by over-arousing the animal" (Coppinger 1970, p. 333). Arousal level must exceed some lower threshold but not exceed an upper threshold in order for a positive (attack) response to be elicited by a given prey item. Such an analysis is in keeping with the theory developed by Dember and Earl (1957) and Dember (1965) to describe how animals respond to external stimuli in the course of their development. In essence they argue that individual animals ignore highly familiar objects, are aroused and curious about objects which are somewhat familiar but slightly different, and avoid those fear eliciting stimuli that are extremely strange.

By increasing a predator's arousal level within limits, normal (familiar) prey movement may also increase the likelihood of an attack response when, at the same time, it interacts with an otherwise familiar and acceptable stimulus. However, movement renders a novel (undesirable) stimulus even less desirable. This could result from increased arousal (via the movement variable) added to the already high arousal associated with unfamiliarity. In this case the upper arousal threshold may be exceeded and the attack response inhibited. It seems logical that a movement-by-unfamiliar interaction might tend to inhibit attack responses while a movement-by-familiar interaction might tend to facilitate an attack response. Awkward movements might increase predator arousal to an even greater extent than normal movement without exceeding the upper threshold. This might occur by virtue of the fact that such prey-associated movements have been paired with success and decreased energy expenditures to procure food.

It is apparent that white pelage is also an undesirable prey characteristic to kestrels which have had no previous experience with it. Similarly, the unfamiliar morph treatment in our experiment represented a novel stimulus, bearing in mind that responses to either or both stimuli were subject to modification as familiarity increased via experience. Attack probability is suppressed by novel (unfamiliar) prey items and conversely enhanced by familiar stimuli, especially ones which have been associated with success. It should be clear, however, that familiarity is relative regardless of the characteristic to which it applies.

The high selection for nonmoving unfamiliar morphs is consistent with arousal theory (e.g., Lindsley 1957) and the optimal level of stimulation concept (Berlyne 1960). An unfamiliar prey item has a high arousal potential. Theoretically, this arousal level is increased by movement and the upper response threshold is exceeded, and thus attack is inhibited. In the absence of added arousal due to movement, an unfamiliar prey item is very acceptable by virtue of a high arousal potential that has not exceeded the upper inhibitory threshold. Furthermore, it would seem unwise for kestrels to freely attack vigorous unfamiliar prey items which weighed up to

one-third or more of their own weight. Snyder (1975) has, in fact, shown this biomass-by-movement parameter to be important in prey selection by a red-tailed hawk. However, attacking unfamiliar prey which show no signs of vitality might be a safe way of accruing experience. This is consistent with, and in support of, Montgomery's (1955) statement of the relationship between fear induced by novel stimulation and exploratory behavior. The experience thus gained could be adaptive in terms of predator familiarity with alternative food sources (Ruggiero 1975).

SUMMARY

Prey selection was assessed based on 116 experimental trials in which six kestrels were presented pairs of mice. Independent variables included pelage color (black and white), morphology (familiar and unfamiliar), and movement (aberrant, normal, and none). Each prey item represented a combination of three treatments, i.e., one per variable.

In general, black pelage was preferred to white and familiar morphology was preferred to unfamiliar. An important interaction occurred between movement and morphology. Kestrel selection was low for moving unfamiliar prey but high for nonmoving unfamiliar prey. The highest rates of attack were elicited by moving familiar prey. It was concluded that movement renders unfamiliar stimuli less acceptable to kestrels while rendering familiar stimuli more acceptable. The acceptability of familiar stimuli was enhanced the greatest when accompanied by aberrant movement.

A summary of kestrel selection preferences with regard to these variables was presented as a prey selection model. When the influence of learning (differential experimental experience) was partially omitted from this independent data set, model accountability increased to 85%. Learning was therefore implicated as an important factor in this kind of experimental research.

Experimental observations were discussed in terms of novelty, and semantic implications of novelty and oddity were considered. The transition of a stimulus from novel to familiar was discussed as a function of learning via experience on the part of the predator.

ACKNOWLEDGMENTS

The authors acknowledge with thanks David Balph, Department of Wildlife Science, for his comments on the original manuscript, and Don Sisson and Charles Romesburg, Department of Applied Statistics, Utah State University, Logan, Utah, for statistical advice. This work was supported by an NDEA predoctoral fellowship to Leonard Ruggiero.

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