

PREY SELECTION BY WILD AMERICAN KESTRELS: THE INFLUENCE OF PREY SIZE AND ACTIVITY

RONALD J. SARNO¹ AND ALAN A. GUBANICH
Department of Biology, University of Nevada, Reno, NV 89557 U.S.A.

ABSTRACT.—Based upon previous reports of high visual acuity in falcons, we hypothesized that prey activity influenced prey selection by American kestrels (*Falco sparverius*) more than prey size. Wild, free-ranging kestrels were simultaneously offered one adult (22–30 g, 3.5–4.0 cm in length) and one juvenile (6–12 g, 2.0–2.5 cm in length) brown laboratory mouse (*Mus musculus*). Mice were presented to kestrels on a 1 × 1 m board with a light-green background marked into 10 × 10 cm squares. To prevent escape, each mouse was tethered to a clear strand of monofilament fishing line. Mouse activity was documented by observing the mice through 8× binoculars and recording the behavior of each mouse into a portable cassette recorder. In trials pairing active mice (large or small) with inactive (dead) mice (large or small), kestrels selected active mice 90% of the time. Kestrels also selected the more active of two mice significantly (regardless of size) in trials which we reduced the activity of one mouse, or in trials which one mouse was naturally less active than the other. These results suggest that within the range of prey sizes used in this study, kestrels select prey on the basis of activity, and exhibit little size discrimination in prey choice decisions.

KEY WORDS: American kestrel; *Falco sparverius*; prey activity; prey selection; prey size; sexual dimorphism.

Selección de presa por *Falco sparverius* silvestres: la influencia del tamaño de la presa y su actividad

RESUMEN.—En base a reportes previos de alta agudeza visual en halcones, hipotetizamos que la actividad de la presa influyó la selección de presas por *Falco sparverius*, más que el tamaño de presa. Se ofreció simultáneamente a individuos de *Falco sparverius*, un adulto (22–30 g 3.5–4.0 cm de largo) y un juvenil (6–12 g 2.0–2.5 cm de largo) de la especie *Mus musculus*. Los ratones fueron presentados en una cubierta de color verde claro de 1 × 1 m, marcada en cuadrados de 10 × 10 cm y ubicada sobre la superficie del suelo. Para evitar el escape de los roedores, se amarraron con una fina lienza de pesca. La actividad de los ratones fue documentada por observaciones con binoculares 8× y registro de la conducta de cada individuo en un tocacinta portátil. En ensayos de ratones activos (grandes o pequeños) con inactivos (muertos), *F. sparverius* seleccionó ratones activos el 90% del tiempo. *F. sparverius* también seleccionó el más activo de los dos ratones (sin hacer caso del tamaño) tanto en ensayos donde reducimos la actividad de uno de los ratones como en ensayos en los que un ratón fue naturalmente menos activo que el otro. Estos resultados sugieren que, dentro del rango de tamaño de presa usado en este estudio, *F. sparverius* selecciona la presa sobre la base de su actividad y exhibe poca discriminación por tamaño al hacer su selección.

[Traducción: Walter S. Prexl y Ronald J. Sarno]

Prey selection by North American raptors has received considerable attention (Brown 1965, Metzgar 1967, Mueller 1968, 1971, 1973, Mueller and Berger 1970, Spiegel et al. 1974, Snyder 1975, Ruggiero et al. 1979, Ruggiero and Cheney 1979). But despite our understanding of responses to various prey stimuli in the laboratory, little is known about what factors influence prey choice under more natural conditions (Drye 1980, Smallwood 1981, 1989, Bryan 1984).

Because American kestrels (*Falco sparverius*) normally respond only to live, moving prey and disregard dead prey (Bird and Palmer 1988), prey activity is an obvious important factor of prey choice. Additionally, foraging theory predicts that prey size should also influence prey selection (Schoener 1969). Laboratory studies of screech-owls (*Otus asio*; Marti and Hogue 1979) and loggerhead shrikes (*Lanius ludovicianus*; Slack 1975) demonstrated that these avian predators show distinct prey size preference.

Field studies of kestrel prey selection by Drye (1980) and Bryan (1984) did not account for the activity of mice used in their trials. Although Small-

¹ Current address: Department of Animal Ecology, Iowa State University, 124 Science II, Ames, IA 50011 U.S.A.

wood (1989) found that kestrels selected the larger mouse of a pair, mouse activity was not measured during those trials. When activity was manipulated, however, only one mouse was offered at a time. Thus, it remains unclear how kestrels respond to size and activity when presented with two prey items simultaneously. The reversed sexual dimorphism of kestrels, combined with the sedentary nature of females during the breeding season (Balgooeyen 1976), could result in different hunting strategies between the sexes, such as size-dependent prey selection or differences in the propensity to initiate selection and/or number of attacks. The objectives of this study were (1) to assess the relative importance of prey size and prey activity as factors influencing prey selection by male and female American kestrels, and (2) to address potential foraging differences between the sexes.

STUDY SITE AND METHODS

This study was conducted in Washoe and Douglas counties, Nevada, from 15 March 1987 to 15 March 1988. To simulate normal prey activity as much as possible, we used live prey in our experiment. Wild, free-ranging American kestrels were simultaneously offered one adult (22–30 g, 3.5–4.0 cm in length) and one juvenile (6–12 g, 2.0–2.5 cm in length) brown laboratory mouse (*Mus musculus*). Mice were presented to kestrels on a 1 × 1 m light-green board marked into 10 × 10 cm squares. To prevent escape, each mouse was tethered around the pectoral girdle with a strand of clear monofilament line (Smallwood 1981). Each monofilament strand passed through a small hole in the center of the board and was attached to a clothespin on the bottom of the board.

The experiment consisted of three trials. Trial one was designed to test kestrel prey selection for active vs. inactive mice, and small versus large mice. Male and female kestrels were offered either a small active mouse and a large inactive (dead) mouse, or a small inactive (dead) mouse and a large active mouse. Mice were euthanized by an intraperitoneal injection of chlorpromazine (Snyder 1975).

Trial two tested kestrel selection for prey (small vs. large) exhibiting different levels of activity. Kestrels were offered either a normally active large mouse and an artificially less-active small mouse, or a normally active small mouse and an artificially less-active large mouse. Mouse activity was manipulated by attaching a long tether (40 cm) to the designated normally active mouse, thus increasing its radius of travel compared to the short tethered (10 cm), artificially less active mouse. Besides reducing the radius of travel, the short tether inhibited mouse activity. The mouse with the short tether was less active in all trials, hence the designation artificially less active. During trial three, both large and small mice were attached to long tethers and permitted unrestrained movement across the trial board. This approach allowed us to investigate possible differences in the rate of movement between large and small mice, thus enabling us to determine which facet

of mouse activity (time of movement or rate of movement) appeared to be more important in eliciting a predatory response by hunting kestrels. Mice that were less active during these trials were designated normally less active.

Kestrels were located while driving through the study area which was primarily agricultural and ranch land dominated by pasture and hay fields. Upon spotting a perched kestrel, the automobile was gradually halted along the roadside or in an adjacent field. Trials began when the board was placed on the ground and the investigator stepped away. The trial board was generally placed 10–50 m (\bar{x} = 36.8 m, SD = 31.1, N = 147) from the automobile in a position allowing kestrels an unobstructed view of the mice. During each trial, mouse activity was observed from the automobile with 8× binoculars. Activity was documented by describing the behavior of each mouse into a portable cassette recorder. For the duration of the trial period, each mouse was assigned to one of two categories: moving (when a mouse crossed one or more squares on the trial board or moved within a 10-cm square), and not moving (when a mouse failed to cross or move within a square). Rate of movement was measured as the number of squares crossed/min. Kestrels were allowed 5 min to initiate an attack. To simulate natural conditions as much as possible, mice chosen by kestrels were automatically released from the board by pulling a string attached to the clothespin and subsequently carried away by the kestrel. If no response occurred within 5 min, the trial was terminated. All trials were terminated in which mice pulled vigorously at their tethers and were not included in the analysis (N = 5). Only the first attacks from all birds that were thought to be presented mice repeatedly were used in the analysis.

Chi-square goodness of fit (Zar 1974) was used to analyze prey choice by males and females. Differences in the activity between mice were analyzed by a Student's *t*-test on the arcsine transformation of the total trial time individuals were moving. The rate of movement of large and small mice was also analyzed by a Student's *t*-test. Due to small sample size for trial one, data for both sexes were combined.

RESULTS

Kestrels exhibited overwhelming selection for active (90% of choices) vs. inactive (dead) mice in trial one (χ^2 = 28.1, df = 1, P = 0.0001) (Table 1). For trial two (large mouse/long tether, normally more active vs. small mouse/short tether, artificially less active or vice versa) female (χ^2 = 12.7, df = 1, P = 0.0004, N = 38) and male kestrels (χ^2 = 11.3, df = 1, P = 0.0008, N = 39) selected normally active mice over artificially less active mice (Table 1). In trial three (small/large mouse long tether) females (χ^2 = 14.6, df = 1, P = 0.0001, N = 41) and males (χ^2 = 18.2, df = 1, P = 0.0001, N = 29) chose the normally more active mouse over the normally less active mouse and showed no selection for size (P > 0.05; Table 1). We found no evidence of differences

Table 1. Number of mice selected by American kestrels during field trials (NA = normally active, NLA = normally less active, ALA = artificially less active; see text for explanation).

		TRIAL 1	
KESTREL SEX	MOUSE SIZE	ACTIVE	INACTIVE
Both	Large	18	0
	Small	13	1
	Total	31	1
		TRIAL 2	
		ACTIVITY	
		NA	ALA
Female	Large	15	3
	Small	15	5
	Total	30	8
Male	Large	15	5
	Small	15	4
	Total	30	9
		TRIAL 3	
		ACTIVITY	
		NA	NLA
Female	Large	18	4
	Small	15	4
	Total	33	8
Male	Large	12	2
	Small	14	1
	Total	26	3

in hunger state between the a.m. and p.m. as there was no selection for either size of mouse in the morning ($\chi^2 = 0.001$, $df = 1$, $P > 0.05$, $N = 64$) or afternoon ($\chi^2 = 0.016$, $df = 1$, $P = >0.05$, $N = 83$). In further support of this observation, no difference was detected in the number of failures to respond to mice between morning and afternoon ($\chi^2 = 0.002$, $df = 1$, $P > 0.05$, $N = 272$).

Differences in the mean percent of trial time spent moving by mice selected (\bar{x} moving time = 19.8, SD = 20.8) and not selected (\bar{x} moving time = 9.6, SD = 12.7) by kestrels were significant ($t = 4.99$, $df = 145$, $P = 0.0001$, $N = 147$). The rate of movement (or the speed that a mouse moved across the board) between large mice ($\bar{x} = 10.9$ squares/min, SD = 11.4) and small mice ($\bar{x} = 10.1$ squares/min, SD = 10.0), however, was not significantly different ($t = 1.47$, $df = 80$, $P = 0.44$, $N = 82$).

Upon being presented with mice, female and male kestrels exhibited no difference in the time that they waited to select a mouse. This trend was consistent throughout fall/winter (female \bar{x} time to select a mouse = 147.0 sec, SD = 106.6; male \bar{x} time to select a mouse = 136.9 sec, SD = 96.7; $t = 2.97$, $df = 69$, $P = 0.38$, $N = 71$), and spring/summer (female \bar{x} time to select a mouse = 146.4 sec, SD = 111.8, male \bar{x} time to select a mouse = 157.9 sec, SD = 96.6; $t = 0.93$, $df = 52$, $P = 0.46$, $N = 54$). Finally, the number of occasions that males and females failed to choose a mouse did not differ during the breeding season ($\chi^2 = 0.01$, $df = 1$, $P > 0.05$, $N = 74$), as well as during the rest of the year ($\chi^2 = 0.002$, $df = 1$, $P > 0.05$, $N = 198$).

DISCUSSION

Our results differ from previous field studies addressing kestrel prey selection (Drye 1980, Smallwood 1981, Bryan 1984). Although the mice used in our study were similar in size to the mice used in earlier studies, none of the previous studies quantified prey activity during trials in which mice were offered to kestrels. In a subsequent study Smallwood (1989) demonstrated significant selection by kestrels for moving mice over nonmoving (drugged) mice when each category of mouse was presented singly to kestrels. He also reported that kestrels selected large mice over small mice in paired presentations because large mice moved at a greater rate.

We, like Smallwood (1989) observed kestrels to select more active mice in all trials. Trial one (small or large inactive mouse versus small or large active mouse) demonstrated most convincingly kestrel selection for active over inactive prey; two mice were presented simultaneously, as opposed to a solitary mouse by Smallwood (1989). Although one could argue that kestrels probably do not commonly encounter two prey items simultaneously under natural conditions, our approach has merit because on occasion birds chose the inactive mouse over the active one. In addition, the mice used in our study did not exhibit size-dependent activity like the mice in Smallwood's (1989) study, which suggests that prey type (e.g., strain) could influence the outcome of studies investigating the role of prey activity in prey choice.

Similar amounts of time to select large and small mice along with an almost identical number of non-responses made by females and males, suggest that both sexes hunt with equal effort throughout the

year and that there appears to be no change in hunting strategy during the breeding season. This interpretation should be considered only within the scope of our experimental design and the population of birds that we were testing.

Although kestrels select more active over inactive or less-active prey, the visual mechanisms involved remain uncertain. Smallwood (1989) speculated that prey characteristics along with size-dependent movement work in concert to elicit an attack, but subsequently added that prey activity is ultimately more important than prey size. This response to prey movement is most likely influenced by the various features of the falconiform eye which appear to be adaptations for improving detection of movement (Hirsch 1982). Within the range of prey sizes used in this study, however, prey size appears to be of little or no consequence in prey choice decisions, and we suggest that if prey size and activity work in concert to elicit an attack, the effect is slight. Future research would benefit from presenting paired mice of equal size that would test selection for active prey without the possible confounding influence of size.

In summary, this study showed that within the range of prey sizes available, kestrels chose prey on the basis of activity, and exhibited little size discrimination in prey choice decisions. Males and females also did not exhibit differences in hunting strategies, at least as we defined them, during different seasons of the year.

ACKNOWLEDGMENTS

Steve Jenkins and Gary Vinyard provided many helpful comments and valuable insights on earlier versions of this draft. The comments of John Smallwood, William Franklin, and two anonymous reviewers substantially improved the manuscript. Ken Helms, Linda Kerley, Pete Rissler, John Basey, and Mike Henry gave helpful suggestions on experimental design, field assistance, and data analysis. The University of Nevada-Reno Department of Agriculture provided a unique area to conduct this study. This study was funded in part by a grant from the University of Nevada-Reno, Department of Biology, graduate student research fund and from a Grant-in-Aid from Sigma Xi, the Scientific Research Society.

LITERATURE CITED

- BALGOOYEN, T.G. 1976. Behavior and ecology of the American kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. *Univ. Calif. Publ. Zool.* 103:1-83.
- BIRD, D.M. AND R.S. PALMER. 1988. American kestrel. Pages 253-290 in R.S. Palmer, [Ed.], Handbook of North American Birds. Vol. 5, Diurnal Raptors (Part 2). Yale Univ. Press, New Haven, CT U.S.A.
- BROWN, L.N. 1965. Selection in a population of house mice containing mutant individuals. *J. Mammal.* 46:461-465.
- BRYAN, J.R. 1984. Factors influencing differential predation on house mice (*Mus musculus*) by American kestrel (*Falco sparverius*). *Raptor Res.* 18:143-147.
- DRYE, P.D. 1980. Prey selection in wild free-ranging American kestrels. M.S. thesis, Univ. North Carolina, Charlotte, NC U.S.A.
- HIRSCH, J. 1982. Falcon visual sensitivity to grating contrast. *Nature* 300:57-58.
- MARTI, C.D. AND J.G. HOGUE. 1979. Selection of prey by size in screech owls. *Auk* 96:319-327.
- METZGAR, L.M. 1967. An experimental comparison of owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *J. Mammal.* 48:387-391.
- MUELLER, H.C. 1968. Prey selection: oddity or conspicuousness? *Nature* 271:92.
- . 1971. Oddity and specific search image more important than conspicuousness in prey selection. *Nature* 233:345-346.
- . 1973. The relationship of hunger to predatory behavior in hawks (*Falco sparverius*) and (*Buteo platypterus*). *Anim. Behav.* 21:513-520.
- AND D.D. BERGER. 1970. Prey preferences in the sharp-shinned hawk: the roles of sex, experience and motivation. *Auk* 87:452-457.
- RUGGIERO, L.F. AND C.D. CHENEY. 1979. Falcons reject unfamiliar prey. *Raptor Res.* 15:33-36.
- , ——— AND F.F. KNOWLTON. 1979. Interacting prey characteristic effects on kestrel predatory behavior. *Am. Nat.* 113:749-757.
- SCHOENER, T.W. 1969. Models of optimal size for solitary predators. *Am. Nat.* 103:277-313.
- SLACK, R.S. 1975. Effects of prey size on loggerhead shrike predation. *Auk* 92:812-814.
- SMALLWOOD, J.A. 1981. Prey size selection by wild American kestrels (*Falco sparverius*) wintering in southcentral Florida. M.S. thesis, Miami Univ., Oxford, OH U.S.A.
- . 1989. Prey preferences of free-ranging American kestrels (*Falco sparverius*). *Anim. Behav.* 38:712-714.
- SNYDER, R.L. 1975. Some prey preference factors for a red-tailed hawk. *Auk* 92:547-552.
- SPIEGEL, R., E. PRICE AND U.W. HUCK. 1974. Differential vulnerability of wild, domestic, and hybrid Norway rats to predation by great horned owls. *J. Mammal* 55:386-392.
- ZAR, J.H. 1974. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, NJ U.S.A.

Received 26 September 1994; accepted 29 January 1995