

(It will be less marked, or absent altogether, if the predator's demands also rise and fall—e.g., if the breeding season of the predator is synchronized with that of its prey.) The selective effect will fall most heavily on the early recruits to the prey population, in circumstances where individual prey grow throughout the season, so that the rate of addition of biomass at the beginning of the season is less than the rate of loss of biomass at the end. The same phenomena might be expected to occur, for example, in predation on larval insects, in which first instar recruits are much smaller than the final instar larvae which leave the population on pupation. Likewise, herbivores might be expected to exert the greatest grazing pressure on the plants that start to grow earliest in the season. The experience of gardeners whose earliest lettuce is eaten by rabbits provides a familiar illustration of the principle.

#### SUMMARY

Nocturnal predators, probably Great Horned Owls, took some adults and many chicks from a large colony of Common Terns in Massachusetts. The adult terns deserted the colony at night, starting early in the laying period. In consequence, incubation periods were unusually long (28 instead of 22 days), about 12% of the eggs failed to hatch, and others were deserted.

The biomass of prey taken each day was roughly constant throughout the season, despite a hundred-fold increase in biomass available. Predators consistently took smaller chicks than the average in the study-plot, and chicks that were already in poor condition. However, they did not consistently take the second and third chicks within each brood, nor chicks from the more exposed nests.

Predation was most intense on the earliest-hatched chicks because of their small numbers and small size. The rate of predation fell from 100% for the chicks hatched in the first four days of the season to 2–3% per day at the end of the season.

Selective predation on early and late breeding individuals is likely to occur whenever the demands of a predator are relatively constant in relation to the seasonal rise and fall in abundance of prey. Predation will fall much more heavily on early than late individuals if individuals grow progressively during the season, so that the biomass of a new recruit to

the population is less than that of an individual leaving the population.

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#### HUNTING BY THE WHITE-TAILED KITE (*ELANUS LEUCURUS*)

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Forty years ago the White-tailed Kite (*Elanus leucurus*) was near extinction in California (Pickwell 1930, 1932), yet today its numbers and range have increased (Morgan 1948, Kimsey 1955, Bolander and Arnold 1965, Eisenmann 1971, G. W. Salt pers.

comm.). These increases probably are due not only to the kites' tolerance of habitat disruption by expanding agriculture (a tolerance apparently uncommon among raptors), but also to the increased abundance of prey species that thrive under agricultural conditions (Krebs 1966). The present study examines the predatory behavior of kites with regard to seasonal variation in hunting habitat, hunting success and strike efficiency, and also the difference between sexes in hunting activities during nesting.

In winter, kites are solitary, diurnal hunters but return to communal roosts each night. Although pairing begins in January, the communal roost is used until nest construction begins in mid-February. Both sexes construct the nest, and both continue to hunt. However, once incubation begins, and until the young approach fledging, the male provides food for both the female and the young.

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TABLE 1. Hunting habitats. Number of hunts, prey strikes, and successful prey strikes made on riparian (R) and on irrigated, cultivated (C) land.

Season	Hunts		Prey strikes		Successful prey strikes	
	(R)	(C)	(R)	(C)	(R)	(C)
Pre-reproductive (Jan. to mid-Feb.)	69	47	25	10	10	7
Reproductive (mid-Feb. to mid-June)	318	67	58	12	36	11
Post-reproductive (mid-June to Aug.)	16	36	0	3	0	3
Total	403	150	83	25	46	21

## METHODS

Field data were collected periodically from January through November 1966 and January through December 1968 near Davis, California in Solano and Yolo counties. Approximately 60 wintering individuals from a single communal roost and eight nesting pairs were observed using 7× binoculars and a 15× spotting scope. Notes were recorded on tape for later transcription.

Kites are not readily sexed by field observation. However, we designate sex on the basis of the assumption that the male always mounts the female during copulation; activities of individuals thus sexed were followed during 26 periods in the months of February through July. Eighty-one hunts were recorded for males and 22 hunts for females. When sex was not determined, activities were recorded simply as those of an adult; this includes all observations of winter kites. Kite hunting habitats were characterized as riparian or irrigated, cultivated land. These birds hunted at the edges as well as the centers of these areas, but it was not possible to determine the amount of hunting over marginal areas such as uncut grasses along roads, irrigation canals or water edges. Kites are easily followed, so we were able to estimate reasonably accurately from U.S. Geological Survey maps (scale = 7.5 min) distances flown to hunt.

Because movements of kites are localized, especially during nesting, observations were not random nor independent within an observation period. Therefore appropriate degrees of freedom for non-independent observations were used in the data analysis (Sokal and Rohlf 1969). Observations are reported as the mean  $\pm$  1 standard error of the mean; N = sample size. To compare daily activity patterns over the study months, all observation times were transformed into the number of hours past dawn, defined here as 35 minutes before sunrise. Temperature data used were recorded at a weather station maintained by the Agricultural Engineering Department, University of California, Davis, which was located centrally within five kilometers of the major observation sites.

## RESULTS

**Hunting areas.** Kites frequent riparian woodlands in the Upper Sonoran life zone during breeding (Miller 1951). Although it is not clear whether they always associate with water, our observations showed that kites rarely are seen far from riparian habitats. Kites also were observed hunting over intermittently irrigated fields of alfalfa, tomatoes, and sugar beets throughout the year (table 1). Kites did not hunt

over cultivated areas with standing water, but they occasionally scavenged in freshly mowed alfalfa and hunted in areas close to where agricultural machinery was used.

Hunting forays extended up to three kilometers from perch sites. However, the most frequent flight distance, primarily of males hunting in riparian areas close to their nest trees, was less than 0.1 km (N = 129). Hunting distances between 0.1 and 1.0 km were less frequent (N = 94), while those greater than one km were least frequent (N = 10).

**Prey.** Remains of only two species, *Microtus californicus* and *Mus musculus*, were found in 125 kite pellets. However, we cannot discount the possibility that other prey were taken since raptors do not produce pellets for all prey eaten (Brooks 1929). Pellets collected under active kite nests contained significantly more ( $P < 0.05$ ) *M. californicus* (63%) than *M. musculus* (36%); pellets collected beneath winter perches and roosts contained almost equal numbers of each species (46% and 52%, respectively). By examination of prey bone size, degree of suture closure, and amount of toothwear, we determined that these kites took prey of many sizes and ages.

**Hunting time.** Kites were considered to be hunting when they flew directly from a perch to an area where they hovered and then returned to a perch. This excludes extensive soaring, agonistic behavior, and occasional hovering while engaged in other flying activity. Under this definition, hunting lasted an average of  $6.1 \pm 0.7$  min (N = 205) in kites of both sexes (table 2) and did not vary significantly with hunting success or season. Kites hunted most frequently from dawn until four hours past dawn and again from 10 until 16 hours past dawn (fig. 1A). This pattern did not vary significantly between nesting and wintering kites.

Hunting occupied varying fractions of the total observation time during different seasons. For example, early in the nesting phase after females had ceased hunting, males spent approximately 12% of the observed time hunting. This percentage for males increased to 15% in April and May when they were supporting both females and juveniles; by June and July, adults of both sexes were hunting independently for the same relative amount of time (5%) as wintering kites.

Because hovering is quite distinct from other types of flight, it is possible to measure the search time (hovering) and the transport time (flying between each hover) separately. The mean number of hovering positions per hunt (N = 48) was  $16.1 \pm 2.2$ , each lasting  $14.2 \pm 0.6$  sec (N = 772). Thus a hunting kite changed hovering positions every 1.2 seconds,

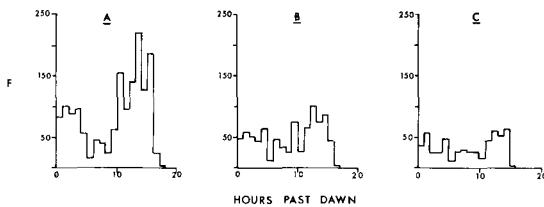


FIGURE 1. Hunting activity over daylight hours throughout the year from observations of 45 kites. F = frequency or total number of observations; A: hunting; B: prey strikes; C: successful prey strikes. Dawn defined as 35 minutes before sunrise.

approximately. Because kites frequently interrupted a hover by dropping a short distance in the air, flights between hover positions were significantly less frequent ( $9.8 \pm 1.9$ ;  $N = 352$ ;  $P < 0.05$ ) than such positions. They also were significantly shorter ( $8.1 \pm 0.5$  sec) than hovering ( $P < 0.05$ ). However, neither the frequency nor duration of flying or hovering differed significantly by sex or with hunting success.

**Hunting success.** Kites typically hunted over open areas, hovering usually about 30 meters above ground and then dropping to three meters before striking. Strikes consisted of short diagonal or vertical falls to the ground. Kites usually fell to the ground feet-first, though some struck head-first. Wings were held in a sharp positive dihedral position. Kites rarely stopped hovering after an unsuccessful prey strike but continued hunting over a number of sites before perching. Most frequently they resumed hovering at the site from which they had just made a prey strike ( $P < 0.001$ ) rather than changing hunting areas. During prey strikes, both male and female kites spent approximately  $0.17 \pm 0.08$  sec ( $N = 85$ ) on the ground whether successful with the strike or not.

Because of the density of the ground cover in most areas, it often was impossible to determine whether a particular prey strike was successful. Therefore, it was recorded as successful only when the kite was observed carrying prey or perching and feeding immediately after a strike. Although prey strikes occurred throughout the day, they were most frequent between nine and 15 hours past dawn (fig. 1B). Success was relatively uniform over all daylight hours (fig. 1C).

The hunting success of kites, defined here as the number of successful prey strikes per hunt was 39% for the entire year. However, success was significantly higher during nesting (mid-February to mid-June; 47%) than at other times of the year (31%;  $P < 0.05$ ). Hunting success did not vary significantly with habitat either within or among seasons. A significant difference ( $P < 0.01$ ) in hunting success was found between males (45%) and females (93%). This probably reflects the fact that males hunted over a greater portion of the year and thus experienced greater variation in prey availability. Strike efficiencies (the number of successes per strike) for males (65%) and females (59%) did not differ significantly. During nesting, however, the strike efficiency in cultivated habitats (91%) was significantly higher ( $P < 0.01$ ) than that in riparian habitats (62%).

**Feeding.** Except for occasional scavenging, kites consumed their prey on elevated perches such as trees, telephone poles and fence posts and therefore were viewed easily while feeding. They did not store prey as reported by Dixon et al. (1957), and the percentage of observation time spent in feeding (7%) did not vary seasonally. The mean feeding time on unshared prey ( $6.2 \pm 0.5$  min;  $N = 125$ ) did not differ significantly between males and females, with time of day, or between nesting and wintering individuals. During nesting, the male shared prey with the female, usually transferring it to her in mid-air. She in turn carried it to the juveniles at the nest. Males

TABLE 2. Hunting and other activities. Mean ( $\pm 1$  Standard Error) duration of activities in minutes, and percent of observation time spent by kites in various activities. N = sample size.

Activity	N	$\bar{x}$ (+ SE)	N	% of observation time <sup>a</sup>
<i>Flying</i>				
hunting				
winter adults	114	6.2 (0.6)	33	11.8
males	76	6.2 (0.6)	17	13.0
females	15	6.0 (0.8)	5	5.3
non-hunting <sup>b</sup>				
winter adults	387	3.6 (0.2)	49	3.6
males	219	3.5 (0.3)	25	8.1
females	122	3.2 (0.3)	21	2.6
<i>Sedentary</i>				
feeding				
winter adults	81	6.6 (0.6)	24	6.8
males	23	5.9 (0.8)	11	5.5
females <sup>c</sup>	21	6.7 (0.8)	12	6.9
perching				
winter adults	638	12.4 (1.2)	54	76.8
males	310	9.0 (1.0)	24	73.9
females	255	15.3 (1.6)	24	84.4

<sup>a</sup> Calculated from five dawn-to-dusk observation days.

<sup>b</sup> Includes gathering of nest materials, nest construction, display flying, copulation, and agonistic interactions.

<sup>c</sup> Includes feeding on prey taken by females or transferred by males but not shared with young.

rarely transferred prey directly to juveniles. The feeding time for males sharing prey was significantly shorter than that for females and juveniles receiving the prey ( $2.3 \pm 0.3$  min vs.  $6.7 \pm 0.8$  min;  $N = 22$ ;  $P < 0.05$ ). Males transferred prey to females as frequently as they fed singly. Wintering kites did not share prey.

**Perching.** Time spent perching, which includes grooming, nest occupation, scanning the ground, and sitting, varied not only by season and with sex, but also with the circumstances of immediate hunting success. Female kites perched up to 95% of the time they were observed during nesting. This was 20% greater than that spent by males during the same observation period. However, by the end of the nesting effort, males' perch time increased to 75–85% of the observation time. Male and female kites differed significantly ( $P < 0.05$ ) in the mean duration of their perching (table 2). Females spent most of their perch time at or actually in the nest, although this activity frequently was interrupted by short flights to and among trees in the nest area. Males perched within sight of the nest but in a nearby tree. Although the relative proportion of time spent perching differed seasonally, the mean duration of perching ( $10.4 \pm 1.2$  min;  $N = 803$ ) did not.

Perch time following unsuccessful hunting was significantly shorter than that after successful hunting and feeding ( $9.6 \pm 1.7$  min vs.  $40.8 \pm 8.8$  min;  $P < 0.01$ ). However, a sequence of two unsuccessful hunts did not further shorten the perch time ( $8.2 \pm 1.2$  min) nor did a sequence of hunting with two successful prey strikes significantly prolong the subsequent perch time ( $41.2 \pm 10.5$  min;  $P < 0.001$ ).

**Non-hunting activities.** Non-hunting activities of the kites, such as nest construction, display flying, copulation, and agonistic interaction showed no frequency relationship with hunting and usually did not occur within 10 minutes of hunting activity. However, copulations occurred closer to the initiation than to the termination of hunting ( $11.7 \pm 0.8$  min vs.  $77.4 \pm 11.5$  min;  $P < 0.05$ ), while nest building by the male was closer to the end of successful hunting and subsequent prey transfer than to the initiation of hunting ( $7.7 \pm 1.7$  min vs.  $16.9 \pm 4.0$  min;  $P < 0.05$ ).

**Environmental effects.** Although rarely active in the rain, kites occasionally hunted in high or gusting winds which easily blew them off hovering sites so that tracking prey appeared difficult. Hunting occurred at all temperatures recorded during the observation period ( $1.1^\circ$  to  $33.3^\circ$  C) but was most frequent at temperatures below  $20^\circ$  C. Prey strikes were most frequent at temperatures between  $10^\circ$  and  $15^\circ$  C, but the number of successful strikes was highest between  $10^\circ$  and  $15^\circ$ , and  $30^\circ$  and  $35^\circ$  C. Non-hunting activities were infrequent between  $22^\circ$  and  $30^\circ$  C.

## DISCUSSION

The recent increase in numbers and range shown by White-tailed Kites has been attributed to the increase in the numbers and range of *M. californicus*. The dependency of this kite on *M. californicus* is considered to be as strict a relationship as that of the Everglade Kite (*Rostrhamus sociabilis plumbeus*) to freshwater snails (Hawbecker 1942). While some raptors show individual preference for certain prey species (Johnston 1956) or for oddity in prey arrays (Mueller 1971), a strict limitation to microtines has not been evident from previous studies of the White-tailed Kite (Bond 1940, 1942, Cunningham 1955,

Dixon et al. 1957, Waian and Stendall 1970). So despite the tendency of this species to frequent certain hunting areas, both its hunting methods, which are discontinuous through the day, and the unpredictability of the prey's presence above-ground (Crowcroft 1955, 1959, Pearson 1960, 1963) argue against the formation of a species-specific search image and for one governed only by restrictions of size and discernable activity.

While the number of prey eaten by predators does not necessarily reflect available prey densities (Craighead and Craighead 1950, 1956, Ivlev 1961, Root 1966), nesting kites did eat more *Microtus* than other prey. These mice, which require free water (Church 1966), probably concentrated in cultivated areas during the dry summer months. Although nesting male kites hunted cultivated areas less frequently than the drier riparian habitats close to their nest sites, they had equivalent hunting success over the two habitats because of higher strike efficiencies on cultivated areas. During the winter, kites showed no preference between hunting habitats and caught almost the same numbers of *M. californicus* as *M. musculus* while spending about a third less time hunting than nesting males. This lack of preference and the similarity in number of prey caught would be consistent with the dispersal of *Microtus* over most habitats during the relatively rainy winters in the Sacramento Valley.

Hunting and prey strikes always increased in frequency toward the end of the day, but kites made successful strikes throughout the day. Therefore, both hunting success and strike efficiency were relatively higher during morning hunting hours. This diurnal hunting pattern varies among raptors, however. Laboratory studies of Kestrels (*Falco sparverius*) show that they kill more prey in the late afternoon while Broad-winged Hawks (*Buteo platypterus*) kill more frequently in the morning (Mueller 1973). One factor influencing the diurnal hunting patterns of kites is the severity of summer day-time temperatures. The low mid-day hunting frequencies accompanied temperatures between  $25^\circ$  and  $35^\circ$  C, but kites did occasionally hunt at temperatures above  $25^\circ$  C. Their relatively higher hunting success at these temperatures may reflect modified prey behavior rather than changes in hunting abilities.

A relationship between predatory behavior and food deprivation in raptors is documented by Mueller (1973), and a similar relationship is seen in the perch time of kites following hunting. For example, male kites after sharing prey and both sexes after unsuccessful hunting had significantly shorter perch time before their next hunts than those which had fed fully.

Approximately two of every five hunts by kites resulted in prey captures (39% hunting success), which, if there are approximately 16 hovers per hunt, would be a success ratio of 2.5%. In comparison, raptors hunting birds had success ratios of 4.5 to 10.8% calculated as the number of prey captured per stoop (Rudebeck 1950, 1951). In terms of the number of successful strikes per strike effort, White-tailed Kites with 62% are more efficient at actually catching prey once a strike has been made, than, for example, a Forster's Tern (*Sterna forsteri*) with a mean percent of prey captures per strike of 24% (Salt and Willard 1971). Apparently then, the exploitation of the abundant prey associated with irrigated fields (Krebs 1966) combined with a high reproductive potential (Eisenmann 1971) are reflected in the numerical increases and widening distributions of the White-tailed Kite in California.

## SUMMARY

This field study of the White-tailed Kite (*Elanus leucurus*) considers seasonal and temporal variations in hunting behavior, hunting success and strike efficiency as well as differences between sexes in hunting activities during nesting. During the winter, adult kites spent nearly 5% of the time hunting. During nesting, after the females had ceased hunting, males hunted for 12% of the time they were observed, increasing this to approximately 15% when supporting juveniles in addition to the nesting female. The duration of hunting did not vary seasonally or by sex. Throughout the year, kites hunted more frequently from dawn to four hours past dawn and from 10 to 16 hours past dawn. Kites made more prey strikes late in the day but were relatively more successful in the morning. Over the year, 39% of the hunts ended in a successful prey strike, and 63% of all strikes were successful. Hunting success was highest during reproduction (47%) when males hunted infrequently in cultivated areas. More *Microtus* (63%) than *Mus* (36%) were caught. At other times, adult kites hunted cultivated and riparian habitats with equal frequency. They had a hunting success of 31% and caught the two prey species with nearly equal frequency.

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