manipulate the prey as described by Ellison (1946). On 15 occasions, birds descended to a perch with insects caught in this manner, and 13 of these were fed to nestlings or fledglings. The type of insect taken was not evident, although the two that I saw most clearly were 1.5–2.5 cm long.

Frequently birds soared very high and I was unable to follow their captures. During 23 episodes where all movements were clearly discernable for at least 1 min, I counted 51 captures in 57 min, giving a capture rate of 0.89/min. This compares favorably with the capture rates for perch- and hover-hunting (0.19 and 0.43 captures/min, respectively) during my study (Rudolph 1982).

Aerial insect-catching was strongly seasonal, and apparently associated with the period when flying insects became abundant. I never observed aerial hunting before 10 May, and 85% of the episodes occurred between 8 June and 8 July, when my study ended [but see Collopy and Koplin 1983—ed.]. To determine whether other factors affected the use of aerial hunting independently of this seasonal effect, I made further comparisons considering only data from the period from 8 June to 8 July, when aerial hunting was occurring and the same potential range of environmental conditions was available for all activities. Temperatures (at 2 m) and wind velocities (at 10 m) for half-hour periods when aerial insect-catching was observed were compared with temperatures and wind velocities for half-hour periods with at least 5 min of hunting behavior of any type. Aerial hunting occurred at warmer temperatures and lower wind speeds than did hunting in general (for temperature, $\bar{x}$ = 29.9°C compared to 27.7°C, $P < 0.05$; for wind speed, $\bar{x}$ = 2.4 m/s compared to 3.2 m/s, $P < 0.01$; t-tests with unequal variances, Snedecor and Cochran 1967). Temperature and wind speed might affect the kestrels' behavior directly, by influencing formation of thermals and the feasibility of soaring flight, or indirectly by altering the abundance of aerial insects.

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DIET, CAPTURE SUCCESS, AND MODE OF HUNTING BY FEMALE AMERICAN KESTRELS IN WINTER

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The hunting behavior and capture success of American Kestrels (*Falco sparverius*) are relatively well known (Jenkins 1970, Sparrowe 1972, Balgooyen 1976, Berdan 1976, Cruz 1976, Bildstein 1978, Rudolph 1983); however, the relationships between diet, foraging mode, and capture success have been addressed only for breeding kestrels (Rudolph 1982). We investigated whether wintering kestrels forage in particular ways in order to capture certain kinds of prey, and whether energetically costlier modes of hunting procure proportionately more of large prey items.

STUDY AREA AND METHODS

Our study was conducted in the Arcata Bottoms, west of Arcata, Humboldt Co., California. This 984-ha area is bordered on the south by Humboldt Bay, on the west by the Pacific Ocean, on the north by the Mad River, and on the east by the city of Arcata and surrounding redwood (*Sequoia sempervirens*) forest. Wheeler and Harris (1970) identified the four major types of land-use in the Arcata Bottoms: permanent pastures (712 ha), hay fields (207 ha), sloughs and remnant tide channels (53 ha), and dikes and roads (12 ha).

We monitored the hunting behavior of seven kestrels on winter feeding territories, four during October 1972–March 1973 and three during September 1973–March 1974. Observations of wintering male kestrels were difficult to obtain since the male:female sex ratio in the Arcata Bottoms was 1:9 (Koplin 1973); therefore, data presented here are restricted to females. Birds were not marked, so some individuals may have been studied in both years. Focal-animal sampling (Altmann 1974) was used to monitor kestrels during dawn-to-dusk observations. Three types of hunting were recognized:

Perch-hunting. Searching for prey from a perch; characterized by frequent turning and bobbing of the head.

TABLE 1. Prey items captured by female American Kestrels during the winters of 1972–1973 and 1973–1974, in northwestern California.

Prey species	Number captured		Percent biomass	
	1972–1973	1973–1974	1972–1973	1973–1974
Invertebrates				
Orthoptera	6	6	1.3	0.8
Coleoptera	11	248	1.5	20.0
Lepidoptera	5	3	0.7	0.3
Lumbricidae	23	153	1.9	7.3
Unidentified invertebrates	211	757	5.1	10.9
Total invertebrates	256	1,167	10.5	39.3
Herpetofauna				
Thamnophis sirtalis	1	4	2.4	5.6
Rana aurora	0	8	0.0	15.9
Hyla regilla	0	16	0.0	8.8
Unidentified frogs	0	6	0.0	7.6
Total herpetofauna	1	34	2.4	37.9
Mammals				
Microtus californicus	7	3	48.1	12.2
Reithrodontomys megalotis	3	0	5.5	0.0
Sorex vagrans	16	5	15.8	2.9
Unidentified mammals	3	4	9.7	7.7
Total mammals	29	12	79.1	22.8
Birds				
Fringillidae	2	0	8.0	0.0
Total captured	288	1,213	100.0	100.0

Hover-hunting. Stationary flapping flight during which the head was oriented downward.

Flight-hunting. Low flapping and soaring flight in which kestrels coursed over fields or chased insects in the air ["aerial insect-catching" of Rudolph 1983—ed.].

All capture attempts were scored as either successful, unsuccessful, or unknown. Hunting success was calculated by dividing the number of successful captures by the total number of completed attempts with known outcomes. When possible, we identified prey when caught; invertebrate prey typically were identified to order. Fresh weights of prey species were obtained from the literature (Wiens 1972, Marti 1974, Balgooyen 1976, Koplin et al. 1980). Relationships among mode of hunting, capture success, and diet of kestrels were analyzed using Chi-square contingency tests (Remington and Schork 1970).

RESULTS AND DISCUSSION

The frequency and biomass of prey species captured by female American Kestrels differed between the two winters of study (Table 1). Greater proportions of invertebrates were captured in the winter of 1973–1974 than in 1972–1973, by both frequency ($\chi^2 = 25.1$, $P < 0.005$) and biomass ($\chi^2 = 125.6$, $P < 0.005$). A comparison between winters of the relative numbers of vertebrate prey showed a shift from predominantly small mammals in 1972–1973, to snakes and frogs in 1973–1974 (by frequency, $\chi^2 = 36.4$, $P < 0.005$; by biomass $\chi^2 = 344.4$, $P < 0.005$).

Inclement weather and periodic flooding of pastures hindered trapping efforts during both winters (Collopy 1975); analysis of available data showed, however, that significantly fewer small mammals were present in 1973–1974 (sign test; $P = 0.03$). The cause of the small mammal decline was unknown, but weather appeared to be an important factor. The winter of 1972–1973 was relatively dry and brought the coldest December temperatures on record, while during the next winter, temperatures were less extreme and rainfall was 45% greater (46.7 inches during October 1973–March 1974; U.S. Dep. Comm. 1972, 1973, 1974). Although invertebrates and herpetofauna were not sampled, they appeared more active during the wetter and warmer second winter. This suggested that the increase in ectothermic prey during 1973–1974 may have reflected an opportunistic response by the kestrels to diminished small mammal densities.

In 1972–1973, 75.8% of all capture attempts ($n = 635$) were initiated from perch-hunts, 8.3% were from flight-hunts, and 15.9% were from hover-hunts. In 1973–1974,

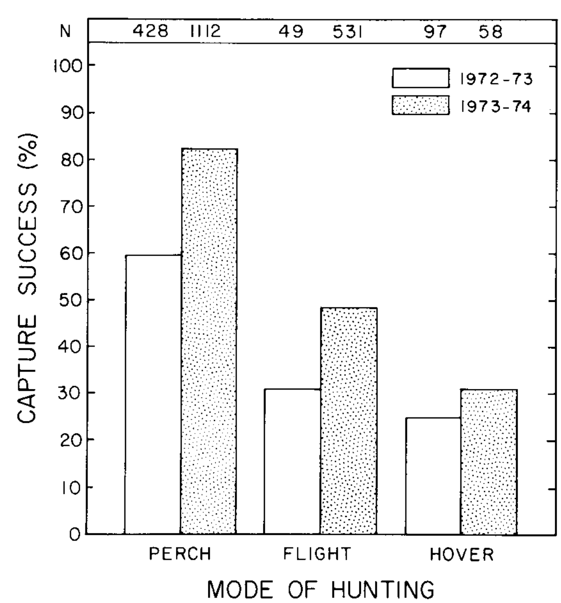

FIGURE 1. Capture success by female American Kestrels in relation to mode of hunting, during the winters of 1972–1973 and 1973–1974 in northwestern California.

TABLE 2. Relative numbers of vertebrate and invertebrate prey of American Kestrels in relation to mode of hunting, during the winters of 1972–1973 and 1973–1974, in northwestern California.

	1972–1973				1973–1974			
	Invertebrate		Vertebrate		Invertebrate		Vertebrate	
Mode of hunting	Number	(%)	Number	(%)	Number	(%)	Number	(%)
Perch-hunt	227	(91.2)	22	(8.8)	894	(95.5)	42	(4.5)
Flight-hunt	12	(80.0)	3	(20.0)	258	(99.6)	1	(0.4)
Hover-hunt	17	(70.8)	7	(29.2)	15	(83.3)	3	(16.7)

70.1% of all capture attempts (n = 1,998) were from perch-hunts, 26.6% were from flight-hunts, and 3.3% were from hover-hunts. The relative number of capture attempts from perch-hunts did not differ between the two winters (χ^2 = 1.3, $P > 0.25$). Significantly more flight-hunts, however, were made in 1973–1974 (χ^2 = 64.3, $P < 0.005$), reflecting the greater number of attempts to capture beetles. Only 11 flying beetles were captured in 1972–1973, whereas 248 were captured during 1973–1974. Proportionately fewer attempts from hover-hunts were made in 1973–1974 than in 1972–1973 (χ^2 = 105.7, $P < 0.005$).

Comparisons between the two winters showed proportionately more invertebrates than vertebrates were captured from perch-hunts (χ^2 = 7.3, $P < 0.001$) and flight-hunts (χ^2 = 27.4, $P < 0.005$) in 1973–1974 (Table 2). The increase in the proportion of invertebrate prey captured in 1973–1974 by perch-hunting kestrels was parallelled by an increase in capture success (χ^2 = 16.5, $P < 0.0005$; Fig. 1). In contrast, capture success while flight-hunting did not differ between winters (χ^2 = 2.3, $P > 0.10$). Finally, no differences between the two winters were detected in either the hunting success (χ^2 = 0.41, $P > 0.50$) or the proportion of the invertebrate prey captured while hover-hunting (χ^2 = 0.89, $P > 0.25$).

Overall, kestrels captured proportionately fewer invertebrates while hover-hunting (76.2%) than while perch-hunting (94.6%; χ^2 = 24.3, $P < 0.005$). Flight-hunting was used almost exclusively to capture flying beetles (259 of 274); moreover, only four vertebrates (1.5%) were captured from flights. Expressing prey capture in terms of relative frequency, however, raises the significance of invertebrates and lowers that of vertebrates (Table 1).

The three hunting methods used by kestrels differ in their energetic cost (King 1974, Koplin et al. 1980). Perch-hunting is considered the least strenuous mode of hunting, flight-hunting is intermediate, while hover-hunting is judged most costly. Data from this study showed that kestrels were largely dependent on vertebrates to meet their energy needs, and that these prey were captured in different proportions depending on the hunting method. The observed pattern of predatory behavior and prey capture appeared to reflect a balance between the energetic cost of the hunting method and the size (or energy content) of the prey. The least costly hunting mode (perch-hunting) allowed kestrels both to capture vertebrates and to opportunistically exploit small but easily caught invertebrates. In contrast, the most costly hunting method (hover-hunting) was associated proportionately less with small invertebrate prey and more with the capture of larger, and therefore more energy-rich, prey.

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