PREY SELECTION BY URBAN-BREEDING MERLINS

NAVJOT S. SODHI^{1,3} AND LYNN W. OLIPHANT²

¹Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, Canada; and ²Department of Veterinary Anatomy, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, Canada

ABSTRACT.—We identified 1,332 items belonging to 36 vertebrate species from prey remains collected near 65 Merlin (Falco columbarius) nests in Saskatoon, Saskatchewan from May to July 1987–1990. Principal prey of breeding Merlins was the House Sparrow (Passer domesticus). They along with the Horned Lark (Eremophilia alpestris) were usually taken more frequently than expected from their relative abundance. Other potential prey species were usually taken in proportion to their relative abundance, or less often than expected. Proportions of adult House Sparrows in the diet decreased while juveniles increased significantly as the Merlin breeding season progressed. During incubation and nestling phases, male and female House Sparrows were taken as expected. In the fledgling phase, Merlins took adult House Sparrows less often and juveniles more often than expected. The relative availability of different species positively correlated with that in the diet during the incubation and nestling phases. Merlins selected prey based on relative availability, independent of prey mass, but not independent of relative abundance. Our data supported the prediction that increase in absolute abundance of selected prey species increased the degree of prey selectivity. Received 12 March 1992, accepted 25 November 1992.

STUDIES OF prey selection in carnivorous predators have concluded that predators either take prey according to their relative abundances (e.g. Jaksic et al. 1981, Nilsson 1981, Turner 1982, Village 1982), or take prey based presumably on relative profitabilities (e.g. Korpimaki 1985, Hunter et al. 1988, Steenhof and Kochert 1988, Canova 1989, Derting and Cranford 1989, Bochenski 1990, Brigham 1990). Predators following the former strategy are called opportunistic feeders, while those following the latter are known as selective feeders (Jaksic 1989). Studies evaluating the species of prey taken usually have considered only prey abundance. Furthermore, few data are available on the sex, age, and size of prey selected by carnivorous predators.

There are many reports of the diet of breeding Merlins (*Falco columbarius*) from North America (Oliphant and McTaggart 1977, Hodson 1978, Becker 1985, Knapton and Sanderson 1985, Laing 1985, James and Smith 1987), but the studies all suffer from small number of nests sampled or a sporadic collection schedule. Better documentation of diet of breeding Merlins comes from Britain (Newton et al. 1984, Bibby 1987). Baker and Bibby (1987) compared relative

abundance of birds (based on questionnaire sur-

the diet of urban-breeding Merlins based on systematic collection of prey remains. Second, we tested the null hypothesis that Merlins would take prey species according to their relative abundance in nature. The alternative hypothesis, based on classical optimal-foraging theory, states that a predator should not take prey species in relation to their relative abundances, but should use cues such as relative profitability (i.e. net energy intake) for prey selection (Emlen 1966, Pulliam 1974). According to the relativeprofitability hypothesis, we predicted that Merlins would not take prey species according to their relative abundances. Also, we considered the effect of relative prey availability (percentage of individuals of each prey species outside of cover) on Merlin prey selection. Third, we examined whether Merlins show prey selectivity according to the sex and age of their primary prey (i.e. House Sparrow as shown in Table 1).

Finally, we examined two qualitative predictions of the foraging-theory prey model, which have been tested in previous studies of other animals (e.g. Schluter 1981, Steenhof and Ko-

veys) in habitats frequented by Merlins with relative consumption of those species by Merlins. They concluded that breeding Merlins took birds in order of their relative abundance. We had three objectives. First, we described

³ Present address: Department of Zoology, University of Alberta, Edmonton T6G 2E9, Canada.

Table 1. Diet of breeding Merlins in Saskatoon, 1987–1990, based on identification of prey remains collected near 65 nests.

		No. ind			_ Percent	Mean percent found at	Percent
Prey species	1987	1988	1989	1990	frequency	nest	biomass
House Sparrow (Passer domesticus)	254	268	164	174	64.5	60.2	55.5
Horned Lark (Eremophila alpestris)	33	23	38	27	9.1	11.4	8.8
American Robin (Turdus migratorius)	18	12	13	15	4.3	4.2	10.5
Swainson's Thrush (Catharus ustulatus)	9	14	13	14	3.7	4.4	3.6
Cedar Waxwing (Bombycilla cedrorum)	12	2	6	15	2.6	2.7	2.6
Chipping Sparrow (Spizella passerina)	6	4	8	11	2.2	2.3	0.9
Yellow Warbler (Dendroica petechia)	6	4	9	7	1.9	1.9	0.6
Snow Bunting (Plectrophenax nivalis)	3	10	5	1	1.4	1.6	1.9
Brewer's Blackbird (Euphagus cyanocephalus)	5	8	3	3	1.4	1.1	2.8
Bohemian Waxwing (B. garrulus)	5	5	5	3	1.3	1.3	2.4
Clay-colored Sparrow (S. pallida)	5	2	1	4	0.9	0.9	0.2
White-throated Sparrow (Zonotrichia albicollis)	1	2	3	3	0.7	0.7	0.5
Hermit Thrush (C. guttatus)	2	3	1	3	0.6	0.6	0.6
Little brown bat (Myotis lucifugus)	0	0	0	7	0.5	0.4	0.2
Others*	19	13	12	16	4.9	_	8.9

^a Less than 0.5% of total including: 5 Savannah Sparrows (Passerculus sanwichensis); 5 Dark-eyed Juncos (Junco hyemalis); 5 Black-capped Chickadees (Parus atricapillus); 4 Least Flycatchers (Empidonax minimus); 4 Rock Dove juveniles (Columbia livia); 4 Lapland Longspurs (Calcarius lapponicus); 4 Mountain Bluebirds (Sialia currucoides); 3 Song Sparrows (Melospiza melodia); 3 Western Kingbirds (Tyrannus verticalis); 3 Hairy Woodpeckers (Picoides villosus); 3 Richardson's ground squirrels (Spermophilus tricolor); 2 Barn Swallows (Hirundo rustica); 2 House Wrens (Troglodytes aedon); 2 Killdeers (Charadrius vociferus); 2 Yellow-rumped Warblers (D. coronata); 2 Blue Jays (Cyanocitta cristata); 2 White-crowned Sparrows, (Z. leucophrys); 1 European Starling (Sturnus vulgaris); 1 Yellow-bellied Sapsucker (Sphyrapicus varius); 1 Red-necked Phalarope (Phalaropus lobatus); 1 Pine Siskin (Carduelis pinus); and 1 Western Meadowlark (Sturnella neglecta).

chert 1988; other references in Stephens and Krebs 1986). This model predicts that when prey abundance is high, a predator should feed only on preferred prey, but when prey abundance declines, it should take a wider variety of prey. Put simply, a predator feeds more selectively when encounters with preferred prey species are frequent (Stephens and Krebs 1986). Also, consumption of different prey species should not be dependent upon their abundance, but on absolute abundance of the most preferred prey. According to this prediction, we should observe an inverse relationship between absolute abundance of the most preferred prey species and diet diversity.

METHODS

We collected prey remains consisting of feathers, feet, mandibles, and heads near 65 Merlin nests from May to July 1987–1990 in Saskatoon, Saskatchewan, Canada (52°07'N, 106°38'W). The study area and Merlin breeding ecology are described by Sodhi et al. (1992). We surveyed 14, 18, 16, and 17 nests once a week during 1987, 1988, 1989, and 1990, respectively. We identified prey remains by comparison with museum specimens in the Department of Biology, University of Saskatchewan. Less than 1% of bird remains could not be identified and were discarded. We iden-

tified House Sparrow heads by sex and age following Robbins et al. (1983) and Nero (1951).

We determined the minimum number of individuals of each species by counting the most frequently occurring body part in each collection. Biomass of each prey species was computed by using average masses reported by Dunning (1984) or those obtained from the museum specimens. When average masses of a species differed between sexes, calculations were made using the mean of sex-specific averages. Following Newton and Marquiss (1982), we arbitrarily assumed juveniles to be two-thirds of the adult mass.

We present three analyses of the food data: relative frequency of prey species (in percentage number or numerical analysis); biomass of prey by species; and mean percentage of a species observed at individual nests. The relative frequencies of prey species give equal weight to each prey species consumed, while the mean percentage of occurrence of a species gives equal weight to each nest investigated (Swanson et al. 1974).

To assess prey abundance, bird counts were made on 12 randomly selected 1-km transects once a month from May to July 1988–1990. Because Merlins feed both in and outside the city (Sodhi and Oliphant 1992), six transects were in each of the feeding areas. Rural transects were selected in areas visited by radio-tagged breeding Merlins. Birds encountered (seen or heard) within 90 m on both sides of the transects were recorded. On average, city and rural transects were completed in 12.5 \pm SD of 1.6 min and 12.7 \pm 2.1 min,

respectively. To maintain consistency each year, bird counts were made in the last 10 days of each month and by one observer (N.S.S.).

The reliability of prey abundance counts was determined by comparing bird censuses made by two independent observers with that of N.S.S. Both these observers initiated bird counts during the first 4 h of daylight in fair weather, 10 min after N.S.S. Observer A and N.S.S. made transect counts in July 1989 on 12 1-km urban transects. Observer B and N.S.S. made transect counts on six 1-km urban transects in July 1990. The relative abundance of potential prey recorded by both independent observers did not differ from that recorded by N.S.S. (chi-square tests, P > 0.05).

We weighted the data on prey abundance by the time spent by hunting Merlins in and outside the city. The time spent by Merlins in each habitat was determined from radio-tracked birds during that year (Sodhi and Oliphant 1992). During different years, at least one individual at 21 to 62% of sampled nests was radio-tracked. Dietary analyses showed that Merlins rarely took bird species with a mass of 100 g or more. Therefore, to calculate potential prey abundance, we only considered bird species with body masses of less than 100 g.

To test for diet selectivity, the relative prey abundance and consumption were compared using Bonferroni's Z-tests if a significant difference between the two was found using chi-square tests (Neu et al. 1974, Byers et al. 1984). We refer to a species eaten less often than expected (based on bird counts) as being avoided and a species eaten more often than expected as being selected or preferred at a probability level of 0.05.

To determine relative prey availability, surveys were made on 12 1-km transects (6 urban, 6 rural; 30 m on both sides were surveyed on each transect) once each month from May to July 1988. Birds were recorded as being in cover (in trees, shrubs, and under low vegetation) or outside cover (on pole, shrub, fence, and roof tops, periphery of trees and shrubs, and flying). Surveys on each transect took 40 min (time determined by conducting six such preliminary transects in April 1988). Previous studies have shown that individual birds outside cover are more vulnerable to predation (Pulliam and Mills 1977, Lima 1990, Watts 1990, Sodhi 1991a). Also, our radio-tracking data showed that of 73 observed Merlin hunting attempts only 2 were on birds in cover ($X^2 = 20.1$, df = 1, P <0.001; expected frequencies for test obtained using prey availability data, 53 for out of cover and 20 for in cover).

The relative prey availability was compared with that in the diet using Kendall's rank-order correlation coefficient (Siegel and Castellan 1988:245–254). For this analysis, we collected sufficient data from prey availability counts (>10 individuals/breeding phase) for nine bird species (House Sparrow, American Rob-

in, Clay-colored Sparrow, Chipping Sparrow, Yellow Warbler, Western Meadowlark, Horned Lark, Savannah Sparrow, and Brewer's Blackbird; scientific names in Table 1).

To determine the age and sex structure of the House Sparrow population, six 1-km urban transects were surveyed once every 15 days (May to July 1990). About 25 min were spent surveying 30 m on both sides of each transect. Individual House Sparrows were identified as males, females, or juveniles, and whether in or outside cover (to estimate availability). The juvenile category was identified based on their yellowish rictus, yellowish legs, and plumage (Summers-Smith 1963). Juveniles exhibit these characters up to four to six weeks after fledging, after which they are difficult to distinguish from adult females (Summers-Smith 1963). In Saskatoon, House Sparrows start fledging from mid-May, but fledging peaks in early June and again in late July (Sodhi et al. 1992). The proportion of females in the House Sparrow population recorded during the Merlin nestling and fledgling phases may be slightly inflated because some juvenile sparrows may have been misidentified as females (Sodhi 1992a). All surveys (prey abundance, prey availability, and House Sparrow age and sex counts) were done on foot on fair-weather days and within the first 4 h of daylight.

We categorized all species encountered on the bird abundance transects into 11 mass classes. The relative abundance and consumption of these classes were compared using the Bonferroni Z-tests to determine prey size selection.

Diet diversity was calculated using the formula: $1/\Sigma$ p_i^2 where p_i is the proportion of prey i in the diet (Levins 1968). Values of this index range from 1 to n (n for equally used resources; see Levins 1968:43). As recommended by Greene and Jaksic (1983), we used species to compute this index.

Data are arranged based on three phases: incubation, nestling, and fledgling. For each nest, these phases were determined by aging the chicks (for details, see Sodhi 1992b) and assuming: a two-day egglaying interval (Sodhi et al. 1993); incubation starting one day prior to laying of the last egg (Sodhi et al. 1993); synchronous hatching within nests (Cramp and Simmons 1980); and fledging at 29 days of age (Becker and Sieg 1985, Oliphant and Tessaro 1985). During the fledgling phase, young are by definition out of the nest, but they remain near the nest and are fed by both parents (Sodhi et al. 1992).

RESULTS

Diet.—Overall, 1,332 prey of 36 vertebrate species were identified (Table 1). Over 99% of prey were birds, with the remainder being mammals. The House Sparrow was the principal prey (Table 1). We encountered House Spar-

TABLE 2. Prey selection (by number killed) by breeding Merlins in Saskatoon. When a species was encountered in the diet, as well as on bird counts, data for it analyzed using Bonferroni Z-test. **

		1988		1989			1990		
Prey species ^c	I	N	F	I	N	F	I	N	F
House Sparrow	Е	S	S	A	Е	E	Α	s	S
Chipping Sparrow	Α	Α	Α	\mathbf{E}^{d}	Α	Α	Α	Α	Α
American Robin	Ε	Α	A^d	Α	E	E	Α	E	E
Cedar Waxwing	В	$\mathbf{E}^{\mathbf{d}}$	N	C	Α	N	S^d	E	N
Yellow Warbler	Α	Α	\mathbf{E}^{d}	C	\mathbf{E}^{d}	\mathbf{A}^{d}	\mathbf{A}^{d}	E	N
Red-winged Blackbird	В	В	В	В	В	N	N	N	N
Black-capped Chickadee	N	$\mathbf{E}^{\mathtt{d}}$	$\mathbf{E}^{\mathtt{d}}$	N	C	N	C	В	N
White-throated Sparrow	E	В	В	C	C	В	$\mathbf{E}^{\mathbf{d}}$	В	N
House Wren	N	N	В	N	N	\mathbf{A}^{d}	N	N	N
Western Meadowlark	N	N	N	N	N	N	$\mathbf{A}^{\mathtt{d}}$	N	N
Savannah Sparrow	E	N	N	N	N	N	\mathbf{E}^{d}	N	N
Horned Lark	S	\mathbf{E}^{d}	S^d	S^d	S^d	S^d	S^d	E	S
Vesper Sparrow	N	N	N	В	В	В	N	В	N
Brewer's Blackbird	E	\mathbf{E}^{d}	\mathbf{E}^{d}	N	N	$\mathbf{E}^{\mathbf{d}}$	N	E	Α
Clay-colored Sparrow	Α	N	N	N	$\mathbf{A}^{\mathtt{d}}$	N	$\mathbf{E}^{\mathbf{d}}$	N	E
Red-eyed Vireo	N	В	В	В	В	В	В	N	В
Swainson's Thrush	C	C	В	C	E	В	C	E	В
Killdeer	В	В	В	В	C	В	В	N	В
Red Crossbill	В	В	В	В	В	В	N	В	В
American Goldfinch	В	В	В	В	N	В	В	В	В
Hairy Woodpecker	В	В	В	C	N	В	В	В	В
Tree Swallow	N	N	В	В	В	В	В	В	В
Brown Thrasher	В	N	В	В	В	В	В	В	В
Red-breasted Nuthatch	N	В	В	В	В	В	В	В	В
Northern Oriole	N	В	В	В	В	В	В	В	В
Barn Swallow	N	В	В	В	C	С	C	В	C
No. prey consumed	159	136	<i>7</i> 5	107	108	67	110	97	96
Diet diversity	3.2	1.3	1.4	4.6	2.2	1.9	8.3	2.0	1.5
Preferred prey									
absolute abundance	6	207	91	1	1	1	4	95	55
Total prey abundance	274	323	130	197	259	161	170	172	108

 $^{^{\}circ}$ (S) selected; (A) avoided; (E) eaten in proportion to abundance; (N) encountered on transects but not eaten; (B) not encountered on transects; and (C) not encountered on transects, but eaten. When S or A, P < 0.05.

row remains at all nests, the percentage ranging from 10 to 93%. The Horned Lark was the second-most-important prey species (Table 1). About 68% of nests had at least one Horned Lark, the percentage ranged from 3 to 69%. These two species represented the most important prey within and among years, although their proportions differed.

Prey abundance and selection.—The relative abundance and consumption of prey species differed significantly in all three breeding phases of all years (chi-square tests, P < 0.05). Only three species were selected—the Horned Lark, House Sparrow, and Cedar Waxwing (Table 2).

For testing qualitative predictions of the prey model, we calculated correlations of the total prey abundance, and of absolute abundance (s) of all selected prey with diet diversity (Table 2). The only significant correlation showed an inverse relationship between absolute abundance of selected prey with diet diversity ($r_s = -0.63$, n = 9, P = 0.04, one-tailed).

Prey availability and selection.—We found a significant positive correlation between relative prey availability and consumption during Merlin incubation and nestling phases (Table 3), but not during the fledgling phase (T = 0.43, n = 6, P = 0.11, one-tailed).

Furthermore, to evaluate whether Merlins selected prey based only on relative prey availability independent of the relative abundance and prey mass, we calculated Kendall's partial

b Data for each year presented for following phases: (I) incubation; (N) nestling; (F) fledgling.

Red-winged Blackbird (Agelaius phoeniceus); Vesper Sparrow (Pooecetes gramineus); Red-eyed Vireo (Vireo olivaceus); Red Crossbill (Loxia curvirostra); American Goldfinch (Carduelis tristis); Tree Swallow (Tachycineta bicolor); Brown Thrasher (Toxostoma rufum); Red-breasted Nuthatch (Sitta canadensis); and Northern Oriole (Icterus galbula). Other scientific names in Table 1.

^d Data not analyzed statistically because of expected frequencies of less than five in more than 20% of cells.

TABLE 3. Kendall's partial rank-order coefficients (with probability in parentheses) for relative prey availability and relative consumption (simple correlation), and controlling relative prey abundance or controlling mass. Simple correlations based on one-tailed and partial correlations on two-tailed tests.

			Controlling for			
Phase	n	Correlation	Relative abundance	Mass		
Incubation	7	0.72 (0.01)	0.39 (>0.20)	0.69 (<0.05)		
Nestling	6	0.83 (0.01)	0.43 (>0.20)	0.85 (<0.02)		

rank-order correlations (Siegel and Castellan 1988:254–262; Table 3). If Merlins selected prey based only on relative prey availability, we expected the correlation between the relative prey availability and consumption to remain significant after relative prey abundance or prey mass was controlled statistically. During both the incubation and nestling phases, Merlins appeared to select prey based on the relative prey availability independent of prey mass, but not independent of relative prey abundance (Table 3).

Size, sex, and age selection.—Merlins usually selected prey that had masses between 21 and 40 g (Table 4). Significantly more male than female House Sparrows were taken by Merlins ($X^2 = 14.8$, df = 1, P < 0.001; Table 5). We could also separate sexes based on plumage color or pattern for two other prey species, and found that Merlins took more male Brewer's Blackbirds (males = 17, females = 2; $X^2 = 10.2$, df = 1, P < 0.01), but more female Yellow Warblers (males = 2, females = 16; $X^2 = 9.0$, df = 1, P < 0.01) than expected were taken (assuming in each case that males and females were equally abundant in nature).

The use of adult House Sparrows decreased while that of juveniles increased seasonally ($X^2 = 77.6$, df = 4, P < 0.001; Table 5). The relative availability of adult House Sparrows decreased, while that of juveniles increased seasonally (Fig. 1). The relative abundance and consumption of different categories of the House Sparrow (male, female, and juvenile) did not differ significantly during the incubation ($X^2 = 0.02$, df = 1, P > 0.20) and nestling phases ($X^2 = 5.6$, df = 2, P > 0.05), but did differ during the fledgling phase ($X^2 = 9.4$, df = 2, Y = 0.01). Both adult sexes were taken less often but juveniles more often than expected by chance during the fledgling phase (Fig. 2).

DISCUSSION

Diet.—Most dietary studies report that breeding Merlins feed mainly on one or two locally abundant bird species. Some studies have documented a small proportion of mammals, insects, and reptiles in the diet (Newton et al. 1984, Becker 1985, Bibby 1987). Three characteristics of the principal prey species seem evident: (a) it is one of the most abundant species;

Table 4. Prey size selection by breeding Merlins in Saskatoon. When a mass category was encountered both in the diet and bird counts, data on it were analyzed using Bonferroni Z-test. For abbreviations, see Table 2.

Prey size		1988			1989			1990		
	I	N	F	I	N	F	I	N	F	
1-10	A	A	Еь	Еь	E		E	Е	Аь	
11-20	E	Α	\mathbf{E}^{b}	Eь	Α	Α	E	E	Α	
21-30	S	S	S	E	S	S	E	S	S	
31-40	S^{b}	Eь	S^{b}	S	S	S ^b	S ^b	E	Еь	
41-50	C	В	В	C	В	В	C	В	В	
51-60	C	В	В	C	В	В	С	В	В	
61-70	\mathbf{E}_{P}	Еь	Еь	E	N	Еь	N	E	S ^b	
71-80	\mathbf{E}	Eь	Еь	E	E	\mathbf{E}^{b}	S	E	E	
81-90	В	В	В	В	В	В	В	В	В	
91-100	N	N	N	N	E	N	\mathbf{E}^{b}	N	N	
>100	N	N	N	N	N	N	N	N	N	

 $^{^{\}circ}$ S and A at P < 0.05

 $^{^{} ext{b}}$ Because of small sample sizes, data not analyzed statistically (i.e. expected frequencies of <5 in >20% cells).

TABLE 5. House Sparrows eaten by Merlins during different breeding phases (1987–1990)^a. Each year, four collection trips per nest made during incubation and nestling phases, whereas only three such trips made during fledgling phase. Therefore, we increased number of male, female, and juveniles collected during fledgling phase by 33%.

Breeding phase	Males	Females	Juveniles
Incubation	57	29	12
Nestling	62	43	74
Fledgling	29	16	102

^{*} Same trend observed in different years; therefore, data pooled.

(b) it leaves cover frequently and, therefore, is vulnerable; and (c) its mass is between 21 and 40 g. In urban habitats of North America, the major prey of Merlins is the House Sparrow (Oliphant and McTaggart 1977, James and Smith 1987, present study), whereas in rural habitats it is the Horned Lark (Hodson 1978, Becker 1985). Similarly, in Europe the chief prey of breeding Merlins is the Meadow Pipit (Anthus pratensis), which has the characteristics noted above (Sperber and Sperber 1963, Bengston 1975, Newton et al. 1978, 1984, Watson 1979, Bibby 1987, Meek 1988).

Newton et al. (1984) acknowledged two biases in food studies based on prey remains collected near the nests. First, pluckings of a certain color or size may be more conspicuous than others. This potential problem can be mini-

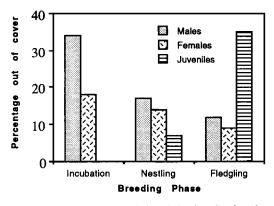


Fig. 1. Relative availability (%) of male, female, and juvenile House Sparrows during different breeding phases of Merlins in Saskatoon during 1990. Sample sizes (out of cover): incubation (males = 81, females = 42); nestling (males = 36, females = 29, juveniles = 14); and fledgling (males = 35, females = 27, juveniles = 104).

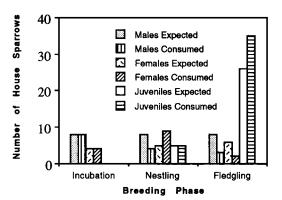


Fig. 2. Comparison between expected and consumed number of male, female, and juvenile House Sparrows during different breeding phases of Merlin in Saskatoon during 1990. Comparison made using chi-square tests, which was only significant (P < 0.05) during fledging phase. During this phase, Bonferroni Z-tests revealed that adult males and adult females were significantly avoided, while juveniles were selected (P < 0.05).

mized by a thorough and systematic search of the nesting area, which we carried out. Second, small prey species may be underrepresented because: (1) Merlins may eat small-sized prey away from the nest (as predicted by central-place foraging theory; Orians and Pearson 1979); or (2) Merlins may wholly consume such prey near the nests, thus leaving no remains. Radio-tracking of breeding Merlins revealed that only 3 House Sparrows of 73 prey captured by foraging Merlins were eaten wholly near the kill sites, while the rest were transported to the nest (Sodhi 1992c). Moreover, near nests we encountered remains of small birds such as Yellow Warblers and Black-capped Chickadees. This suggests that total consumption of a prey near the nest may be affected by factors such as hunger in addition to prey size.

Prey selection.—The Merlin appears to be a selective predator and does not capture prey according to their relative abundances. The two species that were more frequently taken than expected by chance were the Horned Lark and House Sparrow. About 70 to 85% of the individuals of these species were recorded outside cover during different breeding phases. Therefore, both these species may be easier to catch by Merlins (Sodhi et al. 1991).

Species that were usually avoided or taken in proportion to relative abundance had: (1) 45%

or more of their individuals in cover (e.g. Chipping Sparrow and Clay-colored Sparrow); (2) low frequency of occurrence (e.g. Vesper Sparrow); (3) larger size (e.g. Western Meadowlark); (4) inconspicuous plumage (e.g. House Wren); or (5) some combination of these characteristics.

We found that the relative availability of prey species is an important variable affecting prey selection by Merlins. However, we were unable to demonstrate that the relative prey availability had an independent effect on foraging Merlins (Table 3). This may be due to the fact that more individuals of abundant species were out of cover (Sodhi 1991b).

Our data did not support the prediction of increase in prey selectivity at higher prey abundance. Our data did support another prediction of the prey model, that absolute abundance of the selected prey is negatively correlated with overall diet diversity (i.e. degree of prey selectivity increased with increase in absolute abundance of preferred prey).

We found evidence of sex-biased predation by Merlins on the House Sparrow, Yellow Warbler, and Brewer's Blackbird. Sex-biased predation by Merlins and other raptors has been documented previously (Korpimaki 1985, James and Smith 1987, Donazar and Ceballos 1989, Moller 1989, Struhsaker and Leakey 1990). Sexual differences in vulnerability of prev to predation may depend on differences in activity (Geer 1982, Donazar and Ceballos 1989), plumage conspicuousness (Baker and Bibby 1987), size, or body condition (Moller 1989). Male and female House Sparrows were taken as predicted during the incubation and nestling phases, suggesting that relative abundance of sexes may be an important factor causing sex-biased predation (for similar conclusion, see Struhsaker and Leakey 1990).

Merlins fed increasingly on juvenile House Sparrows as their breeding season progressed. Other workers have reported increased predation on juvenile prey individuals as the Merlin breeding season progresses (Newton et al. 1984, Bibby 1987). Juvenile House Sparrows were most abundant and available when Merlins were fledging (Fig. 1). Merlins preyed selectively on juvenile House Sparrows, the most abundant and vulnerable category during the fledgling phase. Similary, Kus et al. (1984) recorded that a wintering female Merlin took proportionally more juvenile Dunlins (*Calidris alpina*) than expected by chance.

ACKNOWLEDGMENTS

We thank G. Peat, J. Freeland, D. Rae, J. Anweiler, R. Beaule, and C. Sodhi for field assistance. We are also grateful to F. Messier, R. Clark, B. Neal, D. Boag, C. White, K. Steenhof, S. Sherrod, G. Schnell, and J. Popp for making comments on this manuscript, and to P. James, P. Thompson, and I. Warkentin for help. This study was supported by a Natural Sciences and Engineering Research Council of Canada grant to L.W.O. and a University of Saskatchewan graduate scholarship to N.S.S.

LITERATURE CITED

- BAKER, R. R., AND C. J. BIBBY. 1987. Merlin Falco columbarius predation and theories of the evolution of bird coloration. Ibis 129:259-263.
- BECKER, D. M. 1985. Food habits of Richardson's Merlin in southeastern Montana. Wilson Bull. 97: 226–230.
- BECKER, D. M., AND C. H. SIEG. 1985. Breeding chronology and reproductive success of Richardson's Merlin in southeastern Montana. Raptor Res. 19: 52–55.
- BENGSTON, S.-A. 1975. Hunting methods and prey of an Icelandic population of Merlin (Falco columbarius). Fauna Flora (Stockh.) 70:8–12.
- Bibby, C. J. 1987. Food habits of breeding Merlins Falco columbarius in Wales. Bird Study 34:64-70.
- BOCHENSKI, Z. 1990. The food of suburban Tawny Owls on the background of birds and mammals occurring in the hunting territory. Acta Zool. Cracov. 33:149-171.
- BRIGHAM, R. M. 1990. Prey selection by big brown bats (*Eptesicus fuscus*) and Common Nighthawks (*Chordeiles minor*). Am. Midl. Nat. 124:73–80.
- Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Classification of a technique for analysis of utilization-availability data. J. Wildl. Manage. 48:1050–1053.
- CANOVA, L. 1989. Influence of snow cover on prey selection by Long-eared Owls Asio otus. Ethol. Ecol. & Evol. 1:367-372.
- CRAMP, S., AND K. E. L. SIMMONS (EDS.). 1980. Handbook of the birds of Europe, the Middle East and North America, vol. 2. Oxford Univ. Press, Oxford.
- DERTING, T. L., AND J. A. CRANFORD. 1989. Physical and behavioral correlates of prey vulnerability to Barn Owl (*Tyto alba*) predation. Am. Midl. Nat. 121:11–20.
- DONAZAR, J. A., AND O. CEBALLOS. 1989. Selective predation by Eagle Owls Bubo bubo on rabbits Oryctolagus cuniculus: Age and sex preferences. Ornis Scand. 20:117-122.
- DUNNING, J. B., Jr. 1984. Body weights of 686 species of North American birds. Monograph 1. Western Bird Banding Association, Cave Creek, Arizona.

- EMLEN, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100:611-617.
- GEER, T. A. 1982. The selection of tits *Parus* spp. by Sparrowhawks *Accipiter nisus*. Ibis 124:159–167.
- Greene, H. W., and F. M. Jaksic. 1983. Food-niche relationships among sympatric predators: Effects of level of prey identification. Oikos 40:151–154.
- HODSON, K. 1978. Prey utilized by Merlins nesting in shortgrass prairies on southern Alberta. Can. Field-Nat. 92:76-77.
- HUNTER, R. E., J. A. CRAWFORD, AND R. E. AMBROSE. 1988. Prey selection by Peregrine Falcons during the nestling stage. J. Wildl. Manage. 52:730–736.
- JAKSIC, F. M. 1989. Opportunism vs selectivity among carnivorous predators that eat mammalian prey: A statistical test of hypotheses. Oikos 56:427-430.
- JAKSIC, F. M., H. W. GREENE, AND J. L. YANEZ. 1981. The guild structure of a community of predatory vertebrates in central Chile. Oecologia 49:21–28.
- JAMES, P. C., AND A. R. SMITH. 1987. Food habits of urban-nesting Merlins Falco columbarius, in Edmonton and Fort Saskatchewan, Alberta. Can. Field-Nat. 101:592-594.
- KNAPTON, R. W., AND C. A. SANDERSON. 1985. Food and feeding behaviour of subarctic-nesting Merlins, *Falco columbarius*, at Churchill, Manitoba. Can. Field-Nat. 99:375–377.
- KORPIMAKI, E. 1985. Prey choice strategies of the Kestrel Falco tinnunculus in relation to available small mammals and other Finnish birds of prey. Ann. Zool. Fenn. 22:91-104.
- Kus, B. E., P. Ashman, G. W. Page, and L. E. Stenzel. 1984. Age-related mortality in a wintering population of Dunlin. Auk 101:69-73.
- LAING, K. 1985. Food habits and breeding biology of Merlins in Denali National Park, Alaska. Raptor Res. 19:42–51.
- LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, New Jersey.
- LIMA, S. L. 1990. Protective cover and the use of space: Different strategies in finches. Oikos 58: 151-158.
- MEEK, E. R. 1988. The breeding ecology and decline of the Merlin *Falco columbarius* in Orkney. Bird Study 35:209–218.
- MOLLER, A. P. 1989. Natural and sexual selection on a plumage signal of status and on morphology in House Sparrows, *Passer domesticus*. J. Evol. Biol. 2:125-140.
- Nero, R. W. 1951. Pattern and rate of cranial "ossification" in the House Sparrow. Wilson Bull. 63:84-88.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541–545.
- Newton, I., and M. Marquiss. 1982. Food, predation and breeding season in Sparrowhawks (*Accipiter nisus*). J. Zool. (Lond.) 197:221–240.

- Newton, I., E. R. Meek, and B. Little. 1978. Breeding ecology of the Merlin in Northumberland. Br. Birds 71:376–398.
- Newton, I., E. R. Meek, and B. Little. 1984. Breeding season foods of Merlins *Falco columbarius* in Northumbria. Bird Study 31:49–56.
- NILSSON, I. N. 1981. Seasonal changes in food of the Long-eared Owl in southern Sweden. Ornis Scand. 12:216–223.
- OLIPHANT, L. W., AND S. McTAGGART. 1977. Prey utilized by urban Merlins. Can. Field-Nat. 91: 190-192.
- OLIPHANT, L. W., AND S. TESSARO. 1985. Growth rates and food consumption of hand-raised Merlins. Raptor Res. 19:79-84.
- ORIANS, G. H., AND N. E. PEARSON. 1979. On the theory of central place foraging. Pages 155–177 in Analysis of ecological systems (D. J. Horn, R. D. Mitchell, and G. R. Stairs, Eds.). Ohio Univ. Press, Columbus, Ohio.
- Pulliam, H. R. 1974. On the theory of optimal diets. Am. Nat. 108:59-74.
- Pulliam, H. R., and G. S. Mills. 1977. The use of space by wintering sparrows. Ecology 58:1393-1399.
- ROBBINS, C. S., B. BRUUN, AND H. S. ZIM. 1983. Birds of North America. Golden Press, New York.
- SCHLUTER, D. 1981. Does the theory of optimal diet apply in complex environments? Am. Nat. 118: 139-147.
- SIEGEL, S., AND N. J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.
- SODHI, N. S. 1991a. Effect of a nesting predator on concealment behaviour of potential prey species. Can. Field-Nat. 105:395–396.
- SODHI, N. S. 1991b. Foraging ecology of urbanbreeding Merlins (*Falco columbarius*). Ph.D. thesis, Univ. Saskatchewan, Saskatoon.
- SODHI, N. S. 1992a. Sex and age differences in risk-taking behavior in House Sparrows. Condor 94: 293–294.
- SODHI, N. S. 1992b. Growth of nestling Merlins, Falco columbarius. Can. Field-Nat. 106:387-389.
- SODHI, N. S. 1992c. Central place foraging and prey preparation by a specialist predator, the Merlin. J. Field Ornithol. 63:71–76.
- SODHI, N. S., P. C. JAMES, I. G. WARKENTIN, AND L. W. OLIPHANT. 1992. Breeding ecology of urban Merlins (Falco columbarius). Can. J. Zool. 70:1477-1483.
- SODHI, N. S., AND L. W. OLIPHANT. 1992. Hunting ranges and habitat use and selection of urban-breeding Merlins. Condor 94:743-749.
- SODHI, N. S., L. W. OLIPHANT, P. C. JAMES, AND I. G.
 WARKENTIN. 1993. Merlin (Falco columbarius).
 Pages 1-20 in Birds of North America, No. 44 (A.
 Poole and F. Gill, Eds.). Acad. Natural Science,

- Philadelphia, and Am. Ornithol. Union, Washington, D.C.
- SODHI, N. S., I. G. WARKENTIN, AND L. W. OLIPHANT. 1991. Hunting techniques and success rates of urban Merlins (Falco columbarius). J. Raptor Res. 25:127-131.
- SPERBER, I., AND C. SPERBER. 1963. Notes on the food consumption of Merlins. Zool. Bidr. Upps. 35: 263-268.
- STEENHOF, K., AND M. N. KOCHERT. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. J. Anim. Ecol. 57:37–48.
- STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, New Jersey.
- STRUHSAKER, T. T., AND M. LEAKEY. 1990. Prey selectivity by Crowned Hawk-Eagle on monkeys in the Kibale Forest, Uganda. Behav. Ecol. Sociobiol. 26:435–443.

- SUMMERS-SMITH, J. D. 1963. The House Sparrow. Collins, London.
- Swanson, G. A., G. L. Krapu, J. C. Bartonek, J. R. Serie, and D. H. Johnson. 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38:302–307.
- Turner, A. K. 1982. Optimal foraging by the Swallow (*Hirundo rustica* L.): Prey size selection. Anim. Behav. 30:862–872.
- VILLAGE, A. 1982. The diet of Kestrels in relation to vole abundance. Bird Study 29:129–138.
- WATSON, J. 1979. Food of Merlins nesting in young conifer forest. Bird Study 26:253–258.
- WATTS, B. D. 1990. Cover use and predator-related mortality in Song and Savannah sparrows. Auk 107:775–778.