HUNTING SUCCESS OF SOME MISSOURI RAPTORS

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ABSTRACT.—Hunting success varied widely among raptors studied throughout Missouri. Higher success rates occurred in raptors hunting relatively small, easily dispatched prey such as invertebrates, herpetofauna, and rodents. "Attacking" raptors, including accipiters and falcons, which concentrated hunting efforts on relatively large, agile prey (mainly birds) were significantly less successful on a per-attack basis. Young raptors were less successful hunters than were adults, and they may have compensated for relatively less developed hunting skills and flight coordination by pursing more invertebrate prey and less agile quarry than did conspecific adults. Intersexual hunting success comparisons in Northern Harriers (*Circus cyaneus*) and American Kestrels (*Falco sparverius*) indicated that males maintain slightly, but not significantly, higher capture rates than females. Females, however, captured larger prey items than their respective mates among 3 species compared (Cooper's Hawks [*Accipiter cooperii*], Northern Harriers, and Red-tailed Hawks [*Buteo jamaicensis*]). Raptors used the most successful hunting method most often, and there was a positive correlation between relative use and rate of success of each hunting strategy. *Received 27 Feb. 1984, accepted 16 Oct. 1985*.

Raptor hunting success varies with season, local weather conditions, habitat characteristics, and prey availability (Brown 1977, Newton 1979, Cade 1982). Hunting success (the percentage of all capture attempts that result in prey capture) also varies according to the age, sex, and species of raptor, as well as with the type of prey hunted. In general, juvenile and immature raptors usually exhibit lower hunting success rates than do adults, and males sometimes display higher success rates than do females (Brown and Amadon 1968, Dekker 1979, Cade 1982). Most male birds of prey are smaller than their female counterparts and they often take smaller prey (Brown 1977, Newton 1979, Cade 1982); thus males may expend less energy per capture than do females (Mosher and Matray 1974, Cade 1982). Additionally, the hunting success rates of "searching" raptors (most insect or rodent eaters) are generally higher than those of "attacking" raptors (pursuers of birds) (Fox 1977). "Searching" raptors spend most of their foraging time looking for small, numerous, relatively easy to catch animals. These raptors capture their prey from a simple, direct attack and are often successful. "Attacking" raptors prey on relatively large, less numerous, more agile animals. They spend less time searching, and their attack is often complex, energy-demanding, and sometimes prolonged (Fox 1977, Cade 1982).

Hunting success rates have been documented for several species of raptors, mostly falcons. Relatively low success rates have been reported

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for raptors that specialize in taking birds, including rates of 5 and 12.8% for the Merlin (*Falco columbarius*) in Europe and California, respectively (Rudebeck 1951, Page and Whitacre 1975). Rudebeck (1951) also reported a combined hunting success rate of 8% for European Sparrowhawks (*Accipiter nisus*), Peregrine Falcons (*F. peregrinus*), and Merlins. An extremely wide range of success rates (7.5–93%) for hunting peregrines has been published (Rudebeck 1951, Brown and Amadon 1968, Parker 1979, Dekker 1980, Treleaven 1980, Cade 1982).

Relatively high success rates of 89 and 82% have been documented for the fish-eating Osprey (*Pandion haliaetus*) in Europe (Brown and Amadon 1968) and North America (Ueoka and Koplin 1973). Success rates of 33– 65% have been reported for the insectivorous and rodent-eating American Kestrel (*F. sparverius*), depending upon season, prey type, and geography (Jenkins 1970, Sparrowe 1972, Rudolph 1982, Collopy and Koplin 1983).

Various success rates have been reported for raptors that feed mostly upon mammals, but supplement their diets with birds and reptiles. Mader (1975) documented a rate of 16% for Harris' Hawks (*Parabuteo unicinc-tus*). Wakeley (1978) reported that Ferruginous Hawks (*Buteo regalis*) were successful 17% of the time in Idaho. Orde and Harrell (1977) reported a success rate of 79% for Red-tailed Hawks (*Buteo jamaicensis*) in South Dakota. Nesting Golden Eagles (*Aquila chrysaetos*) in Idaho were successful on 20% of their capture attempts (Collopy 1983). Clark (1975) calculated a success rate of about 20% for the rodent-specializing Shorteared Owl (*Asio flammeus*).

Here, I report the success rates of Missouri raptors in relation to prey hunted, sex or age of raptor, and hunting methods used.

STUDY AREAS AND METHODS

I collected data on raptor hunting success in various habitats throughout Missouri. Field studies were concentrated in Boone, Callaway, and Cole counties; Table Rock Lake, Duck Creek Wildlife Area, Mingo and Swan Lake National Wildlife Refuges, the greater St. Louis and Kansas City areas, state park and Nature Conservancy prairies in southwest Missouri, and riparian and upland habitats in the Ozarks.

Raptors were observed through $9 \times$ binoculars or a $30 \times$ spotting scope. My observations totaled 3585 h and were divided equally by month over the 7 years of the study. To achieve equal representation throughout the day for all species, observations were made during all daylight hours, including as many full days as possible. Half-day observations were alternated between morning and afternoon. A total of 1064 h (108 days) was accumulated during full-day observations, and the remaining 2521 h were divided equally between morning and afternoon. The number of capture attempts, successful captures, and prey species taken were recorded. All capture attempts with undetermined outcomes were excluded from analysis. Prey were divided into 5 general categories (invertebrates, fish, herptiles, birds, and mammals). All raptors were identified to species. Raptors exhibiting sexual dichromatism were

sexed, including American Kestrels, Merlins, and Northern Harriers (*Circus cyaneus*). I determined age class (adult or immature) for all but Rough-legged Hawks (*B. lagopus*) which could not be aged easily at a distance or under unfavorable lighting conditions. Rough legs exhibit a considerable degree of variability in plumage patterns, further confounded by melanistic individuals which mask characteristics for aging and sexing. I identified immature American Kestrels during summer and fall using plumage characteristics described by Parkes (1955) and Roest (1957). When I was unable to confidently differentiate female and immature Northern Harriers, I placed them in the category of "unidentified brown harrier."

I also recorded the various hunting methods used by raptors including: perch-hunting (Collopy and Koplin 1983), hovering (Brown and Amadon 1968, Brown 1977, Rudolph 1982), flapping flight (quartering, coursing, tail-chasing, and contour-hugging; Brown and Amadon 1968, Brown 1977, Wakeley 1978, Cade 1982), nonflapping flight (soaring, gliding, interhover, and waiting on; Brown 1977, Grubb 1977, Cade 1982), and diving or stooping (Brown 1977, Cade 1982). I calculated the relative use of these hunting strategies by each species by timing the activities of individual birds for 20-min intervals.

RESULTS AND DISCUSSION

Between 1 September 1978 and 31 July 1985, I observed 3266 capture attempts (58% successsful) by 17 species of raptors (Table 1). Of this total, 1512 (46.3%) of the attempts were made by American Kestrels. The four most common Missouri falconiformes (excluding Turkey Vulture, including American Kestrel, Northern Harrier, Rough-legged Hawk, Red-tailed Hawk) accounted for 2577 of 3266 (79.0%) of the hunting attempts during the 7-year period. In addition to being relatively more abundant species, these birds inhabit somewhat open habitat where they are more easily observed.

I recorded success rates ranging from a low of 18.8% for Peregrine Falcons to 69.3% for American Kestrels. Prey, which were divided into five categories, were captured with various success rates by raptors. This apparently was a function of the relative mobility of the prey and the quality of cover in the habitat. Of the five major prey categories, invertebrates (mainly insects) were most easily caught (80.0%). Reptiles and amphibians were also captured relatively easily (77.0%). Raptors had a capture rate of 57.0% when hunting small mammals (mainly mice, rats, squirrels, and rabbits). Fish were captured at a rate of 51.0%, and avian prey at a rate of 20.4%.

Of the 17 species of raptors, Northern Goshawks (A. gentilis) had the highest success rate in capturing birds (33%). The overall success rate (for all raptors) of 20.5% (N = 439) in capturing avian quarry is higher than rates reported by Rudebeck (1951) (7.5 and 5.0%, N = 252, 139), Page and Whitacre (1975) (12.8%, N = 343), and Parker (1979) (16%, N = 116) for Merlins and Peregrine Falcons. Some very high bird-hunting success rates, however, have been reported for Peregrine Falcons by Cade (1982) (93 and 73%, N = 102, 81) and Treleaven (1980) (62%, N = 55)

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and for New Zealand Falcons (*Falco novaeseelandiae*) by Fox (1977) (55%, N = 20). Variation in success rates reported may reflect differences in local weather conditions, seasons, and prey types, or differences in sample sizes.

I compared intersexual hunting success in only two species: American Kestrels and Northern Harriers-the only raptors in Missouri that are sexually dichromatic (except for the Merlin for which the sample was too small). Male kestrels were more successful on a per-strike basis than were females, but there was no significant sex-related difference in hunting bout success ($\chi^2 = 3.46$, df = 1, P > 0.05). Similarly, male harriers were more successful per hunting attempt than were females, but the difference was not statistically significant ($\chi^2 = 3.17$, df = 1, P > 0.05) (Table 1). Higher hunting success rates of males may be an adaptation for the successful provisioning of females and young throughout most of the nesting season (Cade 1982). Females may make up for their lower rate of capture by catching larger quarry than the smaller males can. During nesting, larger prey items were consistently captured by the females of breeding pairs of Cooper's Hawks (A. cooperii; Toland, in press a), Northern Harriers (Toland, in press b), and Red-tailed Hawks (Toland, unpubl. data) in Missouri. By transporting larger energy packages, a female actually may be more efficient than her mate in terms of energy used per unit of energy gained (Cade 1982).

Immatures were less successful hunters than adult raptors for 8 of the 9 species (Table 1). Adult Bald Eagles (Haliaeetus leucocephalus) were significantly more successful per strike than were immatures ($\chi^2 = 7.14$, df = 1, P < 0.01). Hunting bout success in adult American Kestrels (males and females combined) was significantly greater than in immatures ($\chi^2 =$ 7.22, df = 1, P < 0.01). Adult Red-tailed Hawks were significantly more successful per capture attempt than immatures ($\chi^2 = 7.10$, df = 1, P < 0.01). Swainson's Hawk (B. swainsoni) adults were more successful than immatures, but the small sample size precluded statistical significance. Among Broad-winged Hawks (B. platypterus) and Red-shouldered Hawks (B. lineatus) adults were more successful hunters than immatures, but the differences were not significant ($\chi^2 = 0.33$, df = 1, P > 0.05; $\chi^2 = 0.40$, df = 1, P > 0.05). Unsexed juvenile Northern Harriers were less successful per capture attempt than were either adult males or females, but the difference was not significant ($\chi^2 = 2.01$, df = 1, P > 0.05). Adult Cooper's Hawks were more successful than immatures, although the difference was not significant ($\chi^2 = 0.67$, df = 1, P > 0.05).

Immature Sharp-shinned Hawks (A. striatus) exhibited a higher hunting success rate than adults, but the sample was too small to test statistically. The relatively high success rates of immature Sharp-shinned Hawks, as

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TABLE 1	RAPTORS,
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71.9 67.4 54.5 25.0 33.8 41.2 30.7 27.5 18.8 25.0 25.0 30.0 33.3 24.0 69.3 21.4 12.5 26.5 30.0 33.3 31.3 % Overall hunting success Total no. attempts 1512 610 136 834 68 ø 4 16 × ø 24 10 70 45 25 9 411 131 75 69 (25.0)(18.8) (25.0) (20.0)(25.0)(14.1)(21.9) (10.0)43/133 (32.0) 32/89 (36.0) 11/44 (25.0) (21.4) (12.5) (15.4)(12.1) (20.7) (33.3) (0.0) (0.0) (0.0) Birds ۱ 3/16 2/20 3/14 6/30 6/24 6/39 6/29 13/92 7/32 4/33 0/10 2/8 2/8 3/9 1/8 0/0 2/0 (34.0) (25.0) (0.0) (20.0)(70.0)(42.3) (53.3) (27.3)(33.7) (41.0)(65.0) (31.0)Small mammals 302/430 176/294 I 91/270 I I 1 1 I 480/734 2/10 36/88 17/50 12/48 8/15 3/11 11/26 26/84 No. successful captures/no. attempts (%) (100.0)(100.0)(100.0)(0.68) (87.5) (66.7) (66.7) (6/35 (74.3) 9/11 (81.8) 9/12 (75.0) Reptiles and amphibians Prey taken ł I I L ļ I I I 1 2/3 8/6 2/8 1/1 1/1 1/1 Fish L I T 1 1 I 1 1 1 ۱ I I 1 I I I I 1 I 1 (100.0) (100.0)(75.0) (80.0) (20.0)259/307 (84.4) 223/272 (82.0) 517/638 (81.0) 35/58 (60.0) 3/4 (75.0) 3/4 (75.0) 3/4 (75.0) 9/14 (64.3) Invertebrates I L I 1 Ł I 3/4 2/2 1/5 4/5 2/2 Unidentified brown Sharp-shinned Hawk Northern Goshawk American Kestrel Northern Harrier Peregrine Falcon Merlins (adults) Cooper's Hawk Species Prairie Falcon Immatures Immatures mmatures Immatures Immatures harriers Females Females (adults) Adults Adults (adults) Adults Males Males

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58.0 43.3 61.0 62.5 57.0 50.6 56.4 54.0 58.8 53.8 66.2 67.3 63.2 59.0 55.6 67.0 30.0 40.8 21.6 66.7 8 Overall hunting success Total no. attempts 60 3264 465 250 215 80 54 26 52 19 14 189 106 173 76 97 2 71 22 (25.0)90/439 (20.5) (15.8) (16.7) (20.0)(14.3) 2/16 (12.5) (4.0) (0.0) (0.0) (0.0) (0.0) 0/3 (0.0) (0.0) 3/41 (7.3) Birds ١ 1 T I 1/25 6/30 1/4 6/38 0/4 0/8 17 1/6 0/1 0/1 0/1 26/57 (45.6) 984/1719 (57.0) 12/17 (70.6) (62.4)(52.3) (53.8) (58.3) (46.7) (57.1) (61.0) (40.0)(46.2) (50.0)(43.0)(56.0)(53.3)(53.3)(70.8) Small mammals 8/15 8/15 31/185 81/155 01/180 212/340 21/39 7/15 6/13 14/24 16/28 [4/23 2/5 3/6 3/7 No. successful captures/no. attempts (%) 1/1 (100.0) 77/100 (77.0) (85.0) (33.3) (73.7) (75.0) (66.7) (75.0)(75.0)(78.3)Reptiles and amphibians Prey taken I 1 I L ١ I L I ł 14/19 9/12 9/12 17/20 12/16 2/3 8/23 1/3 115/226 (51.0) (66.7) (66.7) 71/106 (67.0) 41/117 (35.0) 29/60 (48.3) (2/57 (21.0) Fish ļ I 1 ł I 2/3 (100.0)2/2 (100.0) 622/782 (80.0) (77.8) (71.4)(80.0) (71.4) (73.3) (75.0)(71.4)(69.4) (72.0)(83.3) (73.3)(75.0) Invertebrates ١ 1 I 1 10/14 10/12 22/30 34/49 11/15 12/16 44/61 6/1 6/8 2/2 4/5 5/7 5/7 Red-shouldered Hawk Broad-winged Hawk Rough-legged Hawk Great Horned Owl Swainson's Hawk Red-tailed Hawk Short-eared Owl Osprey (adults) Species Immatures Immatures Immatures Immatures Immatures **Bald Eagle** All species Adults (adults) (adults) Adults Adults Adults Adults

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well as immatures of other species, may result from immatures concentrating on smaller, more numerous, and more easily caught invertebrate prey. Excluding Bald Eagles and American Kestrels, immatures of 7 raptor species attacked invertebrates on 90 of 386 (23%) capture attempts while adults of these species pursued invertebrates only during 45 of 700 (6.4%) capture attempts. Conversely, capture of relatively large, less numerous, agile avian prey was attempted by adult raptors on 179 of 700 (25.6%) hunting bouts, but by immatures on only 41 of 386 (10.5%) attempts. Overall, immatures were successful on 237 of 551 (43%) capture attempts, in contrast to a success rate of 63% (1,404 of 2,220) for adults.

There was no significant difference in hunting success among congeneric buteos ($\chi^2 = 3.13$, df = 4, P > 0.05), accipiters ($\chi^2 = 0.14$, df = 2, P > 0.05), or the 3 larger falcons ($\chi^2 = 0.12$, df = 2, P > 0.05). As a group, buteos were significantly more successful hunters on a per-strike basis than either accipiters ($\chi^2 = 37.31$, df = 1, P < 0.001) or the larger falcons ($\chi^2 = 22.12$, df = 1, P < 0.01). American Kestrels were significantly more successful per capture attempt than the larger falcons ($\chi^2 = 40.55$, df = 1, P < 0.001). These differences were apparently due to the hunting methods used and prey types pursued by these groupings of searching and attacking raptors. There was no significant difference in hunting success between the 2 groups of attackers, namely, accipiters and larger falcons ($\chi^2 = 0.86$, df = 1, P > 0.05).

Of the 17 species of raptors studied, 11 were categorized as "searchers" (Fox 1977, Cade 1982). When they were combined, these 11 species accounted for 3115 of 3266 (95%) of the total hunting attempts. Searching raptors spend much of the time hunting from a relatively conspicuous perch or hover, or while systematically searching from coursing, slow, horizontal flight, and prey predominantly upon invertebrates and small mammals (Cade 1982). The hunting success of this group of raptors averaged 59%, significantly higher than the average hunting success of 27% for the "attackers," which included Northern Goshawk, Cooper's Hawk, Sharp-shinned Hawk, Peregrine Falcon, Prairie Falcon (F. mexicanus), and Merlin ($\chi^2 = 28.28$, df = 1, P < 0.01). Although they fit the searcher category, Northern Harriers were significantly less successful per attack than were buteos ($\chi^2 = 71.55$, df = 1, P < 0.001) and they exhibited hunting success similar to the 6 attackers ($\chi^2 = 2.05$, df = 1, P > 0.05). The relatively low success rate of harriers when compared to other searchers is probably a result of their atypical foraging behavior (Rice 1982). Comparative anatomical research indicates a strong convergence of the facial anatomy of harriers with that of owls (Clark and Stanley 1976). The facial ruff and associated structures, as well as the low foraging flight of both

harriers and certain owls, suggest a reliance by harriers on auditory cues when hunting (Rice 1982). Because hunting harriers often strike at prey that they probably hear but cannot see, their success may be lower than sight-hunting raptors with similar food habits. Short-eared Owls, which use similar foraging methods and habitat as Northern Harriers, had similar hunting success ($\chi^2 = 2.09$, df = 1, P > 0.05).

Observations of foraging raptors in these two general groupings indicated that hunting success varied according to agility of prey and size of prey relative to size of raptor. The size of prey taken by "attacking" species in Missouri averaged from 25 to 50% of the body weights of the raptors, while "searching" species took prey averaging only 5–10% of their body weights (Toland, unpubl. data). Birds (the most agile prey group) comprised 56% (23 of 41) of the successful prey captures by the 6 raptors categorized as attackers. Raptors in the searcher group captured birds on 67 of 1846 (3.6%) successful captures.

The hunting method used most frequently by each raptor was the one that resulted in the highest hunting success for each. For example, American Kestrels perch-hunted 88% of the time but only hover-hunted 10% of the time. They used flapping flight (contour-hugging and tail-chasing) and stooping only 2% of the time. Their hunting success rates for the 3 methods were 76, 52, and 45%, respectively ($\chi^2 = 79.36$, df = 2, P < 0.001; Toland 1983).

Buteos used perch-hunting 72%, nonflapping flight 13%, hovering 8%, and flapping flight 7% of the time. Broad-winged Hawks spent the most time perch-hunting (92%), and Rough-legged Hawks hover-hunted the most (11%). Buteos as a group were successful on nearly 60% of their capture attempts, including 71% from a perch, 50% from a hover, 25% from a glide or soar, and 18% from flapping flight.

Ospreys hunted most often from a hover (44%), followed by nonflapping flight (36%), and perch-hunting (20%). Ospreys were 75% successful when hunting from a hover, but only 55% successful when gliding or soaring, and 33% when perch-hunting. Bald Eagles used gliding and soaring, perchhunting, and flapping flight 41, 34, and 25% of the time, respectively. Eagles were successful capturing quarry 34% of the time from nonflapping flight, 30% from a perch, and 25% from flapping flight.

Accipiters initiated 60% of their attacks from fast horizontal flapping flight (mostly contour-hugging), and hunted from a perch 40% of the time. As a group, accipiters captured their quarry 33% of the time, 35% of the time from flapping flights, and 30% of the time from a perch.

Northern Harriers hunted from a slow coursing and quartering flight more than 96% of the time. They occasionally perch-hunted from a small tree, bush, fence post, or on the ground. Only 9 capture attempts by Northern Harriers were initiated from a perch: 33% were successful.

The 3 larger falcons used fast flapping flight (tail-chasing, coursing, and contour-hugging) and stoops during capture attempts virtually 100% of the time. As a group they had the lowest hunting success (21%).

Short-eared Owls hunted from coursing, slow flapping flight on all of the hunting bouts I observed. Conversely, Great Horned Owls initiated all of their capture attempts from a perch.

There was a positive correlation between relative use and capture success of hunting methods used by all raptor species (r = 0.69, P < 0.05). Similar results have been reported by Sparrowe (1972), Collopy and Koplin (1983), and Rudolph (1982) for American Kestrels, Shrubb (1982) for Common Kestrels (*F. tinnunculus*), and Grubb (1977) for Ospreys.

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