# FORAGING BEHAVIOR OF NORTHERN HARRIERS WINTERING IN SOUTHEASTERN SALT AND FRESHWATER MARSHES

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ABSTRACT.—We conducted a comparative study of the foraging behavior, hunting success, and diet of wintering Northern Harriers (*Circus cyaneus*) at North Inlet Marsh, a salt marsh in South Carolina, and Paynes Prairie, a freshwater marsh in Florida. The relative use of five hunting methods in the salt and freshwater marshes differed significantly ($P < 0.0005$). Harrier pouncing rates at Paynes Prairie were three times greater than at North Inlet Marsh, but their hunting success was significantly less (5.8% vs. 15.1%, $P < 0.0005$). Greater capture success at North Inlet Marsh was caused by differences in diet and vegetation structure rather than by differential use of hunting techniques. Harriers hunting at North Inlet Marsh captured exclusively birds, whereas at Paynes Prairie harriers captured primarily cotton rats (*Sigmodon hispidus*). Although differences in pouncing rate, capture success, and diet occurred between the two study areas, prey capture rates at North Inlet Marsh (27 g/h) and Paynes Prairie (23 g/h) were similar. Our finding that harriers had higher capture success hunting small- and medium-size birds on a salt marsh than cotton rats on a freshwater marsh contradicts the generalization that more mobile prey are more difficult to capture and illustrates the importance of comparative foraging studies. *Received 3 January 1986, accepted 4 May 1986. accepted 4 May 1986.*

NORTHERN Harriers (*Circus cyaneus*) winter in a variety of habitats in North America, including pasturelands, croplands, dry plains, unforested uplands, estuaries, and freshwater marshes (Brown and Amadon 1968, Bildstein in press). As a consequence of this widespread distribution, their diet varies. Small rodents are the typical winter food in many areas (see Clark and Ward 1974, Sherrod 1978 for reviews). Craighead and Craighead (1956) found meadow voles (*Microtus pennsylvanicus*) comprised over 90% of the winter diet of harriers in Michigan. In Ohio, however, birds comprised 40% of the prey taken by males and 4% of the prey taken by females; meadow voles comprised most of the remainder (Bildstein 1978). In the southeastern United States, cotton rats (*Sigmodon hispidus*) are an important winter food in freshwater marshes (Jackson et al. 1972), while in coastal salt marshes, marsh rabbits (*Sylvilagus palustris*; Tomkins *in* Bent 1938) and Clapper Rails (*Rallus longirostris*; Sprunt and Chamberlain 1970, Bildstein pers. obs.) often are important.

Schipper et al. (1975) reported that diet and hunting behavior of Hen Harriers (*C. cyaneus cyaneus*) wintering in Europe varied with habitat and that sexual differences existed in foraging behavior. In North America there have been no comparative studies that examine the influence of winter habitat and prey taxa on the hunting behavior of Northern Harriers. We compared the foraging behavior, hunting success, and diet of harriers wintering in salt and freshwater marshes, two important wintering habitats in the southeastern United States.

## STUDY AREA AND METHODS

We observed Northern Harriers hunting over a salt marsh in South Carolina and a freshwater marsh in Florida. North Inlet Marsh (NIM) is a 3,000-ha, high-salinity salt marsh 6 km east of Georgetown, South Carolina. The site is approximately 60% *Spartina alterniflora* salt marsh; 10% mud flats, sandbars, and oyster reefs; and 30% open water (Forth 1978). Paynes Prairie (PP), 3 km south of Gainesville, Florida, is a 5,600-ha basin that contains plant communities characteristic of freshwater marshes, wet meadows, and pastures (Easterday 1982). Harriers on Paynes Prairie typically were found in wet meadows dominated by

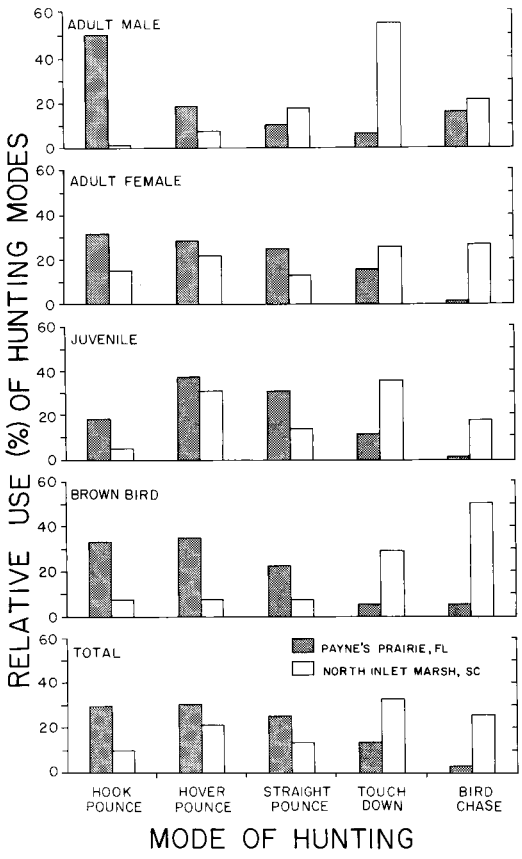


Fig. 1. Relative use of different hunting methods by wintering Northern Harriers in relation to sex and age class.

maidencane (*Panicum hemitomon*) and southern cutgrass (*Leersia hexandra*), and in pastures dominated by broomsedge (*Andropogon virginicus*).

In South Carolina, we observed harriers during the winters of 1979–1980, 1980–1981, 1981–1982, and 1983–1984 from a stationary 18.5-m tower in the middle of the marsh. In Florida, we observed birds during the winters of 1982–1983 and 1983–1984 from a 3-m tower mounted on the back of a truck.

At both study sites, individuals were selected as they flew into view and were observed using focal-animal sampling (Altmann 1974). Harriers were observed until they flew from view or until dark. Observations of individual harriers ranged from <1 min to >8 h. Sex and age class (adult or juvenile) of each harrier were determined using criteria reported by Brown and Amadon (1968) and Bildstein (in press). Individuals that we were unable to classify (i.e. some adult females and juveniles of either sex) were recorded as "brown birds."

During each observation we recorded the amount of time the bird spent perching, hunting in flight, soaring, carrying prey, and feeding. The method of hunting, number of pounces, and prey species captured by each harrier also were recorded. Each pounce was considered an independent capture attempt. Hunting success was calculated by dividing the number of successful captures by the total number of completed attempts with known outcomes. At both study sites harriers took prey only while flying. Five types of pounces were observed; these included hook pounces, hover pounces, straight pounces, touch downs, and bird chases (cf. Bildstein 1978, in press). Estimates of the biomass of prey captured daily by harriers were calculated using data collected on hunting success and prey masses obtained from the literature (Clench and Leberman 1978, Maehr 1980, Terres 1980, Steenhof 1983, J. Cox pers. comm., N. Holler pers. comm.). Statistical comparisons of the hunting success of harriers in relation to site and mode of hunting were performed using Chi-square contingency tests (Remington and Schork 1970).

## RESULTS

In South Carolina, we observed harriers 298 times for a total of 105.7 h. Birds hunted during 33.8% (35.8 h) of the total observation period. At Paynes Prairie in Florida, harriers were observed 199 times for a total of 148.8 h; hunting occurred during 27.2% (40.5 h) of the total period of observation.

Harriers hunting at Paynes Prairie used hook, hover, and straight pounces on 84% of the capture attempts (576 of 687); touch downs and bird chases comprised the remaining 16% (Fig. 1). The relative use of the five hunting modes at North Inlet Marsh was significantly different from that at Paynes Prairie ($\chi^2 = 173.8$, $P < 0.0005$), with hook, hover, and straight pounces accounting for 43% of the capture attempts (88 of 205); touch downs and bird chases were much more prevalent on the salt marsh, where they accounted for 57% of the capture attempts. Significant differences in the relative use of hunting modes by harriers wintering in the salt and freshwater marshes were apparent for each sex and age class analyzed ($P < 0.0005$, Fig. 1).

Overall, harriers at Paynes Prairie pounced three times more frequently per hour of hunting than those at North Inlet Marsh, although adult males pounced at similar rates at both sites (Table 1). Adult females and juveniles at Paynes Prairie pounced several times more frequently than their counterparts in South Carolina.

Hunting success differed significantly ($\chi^2 = 18.8$, $P < 0.0005$) between the two study areas

TABLE 1. Pouncing rates and hunting success of Northern Harriers wintering on North Inlet Marsh, South Carolina, and Paynes Prairie, Florida.

| Sex/age class | North Inlet Marsh | | | Paynes Prairie | | |
|---|---|---|---|---|---|---|
| | No. of pounces | Pouncing rate (no./h of hunting) | Hunting success[a] (%) | No. of pounces | Pouncing rate (no./h of hunting) | Hunting success[a] (%) |
| Adult male | 29 | 9.0 | 3.4 | 52 | 7.8 | 9.6 |
| Adult female | 114 | 5.6 | 18.4 | 397 | 21.9 | 4.8 |
| Juvenile | 48 | 5.3 | 10.4 | 165 | 18.0 | 6.7 |
| Brown bird[b] | 14 | 4.4 | 28.6 | 73 | 11.2 | 8.2 |
| Total | 205 | 5.7 | 15.1 | 687 | 17.0 | 5.8 |

[a] On a per-pounce basis.
[b] Includes adult females and juveniles of both sexes.

(Table 1); at North Inlet Marsh, harriers captured prey on 15.1% of their pounces, while at Paynes Prairie they were successful on 5.8% of their attempts. Adult female harriers had significantly greater hunting success at North Inlet Marsh than at Paynes Prairie (18.4 vs. 4.8%; $\chi^2 = 22.8$, $P < 0.0005$). Juveniles at North Inlet Marsh also tended to be more successful at prey capture than those at Paynes Prairie (10.4 vs. 6.7%), although the difference was not significant ($\chi^2 = 0.8$, $P > 0.30$). The small number of attempts at capture made by adult males and brown birds makes site and sex comparisons tenuous.

Differences in the hunting success of harriers wintering at the two sites were due to the consistently higher success rates of harriers at North Inlet Marsh, regardless of pouncing method (Table 2). Harriers observed hook pouncing, hover pouncing, and straight pouncing on North Inlet Marsh had significantly greater hunting success rates than birds on Paynes Prairie. Touch downs, typically a slow, deliberate descent onto wracks of dead floating vegetation (NIM) or onto rodent nests (PP), rarely resulted in prey capture. The lack of a significant difference in hunting success of harriers chasing birds at the two study sites suggests that when avian prey is flushed and pursuit is initiated, the likelihood of capture is similar in both habitats.

Differences in hunting success on a per-pounce basis between harriers wintering in salt and freshwater marsh habitats appear to be influenced by differences in the prey taken (Table 3). Harriers hunting at North Inlet Marsh captured small- and medium-size birds exclusively. This apparently was the result of an absence of diurnally active small mammals in the salt marsh habitat (Pfeiffer and Wiegert 1981). At Paynes Prairie, high vegetation often concealed distant harriers once they landed and fed on the ground, and prevented identification of 55% of the prey. Cotton rats (*Sigmodon hispidus*) comprised the majority (67%, $n = 12$) of those prey identified. One snake and four small passerines also were captured.

Overall, capture rates, whether expressed as the number/hour of hunting or number/hour of total observation, were similar in the two habitats (Table 4). Likewise, mean prey masses at North Inlet Marsh (92.7 g) and at Paynes

TABLE 2. Hunting success of Northern Harriers wintering in North Inlet Marsh, South Carolina, and Paynes Prairie, Florida, in relation to method of hunting.

| Method of hunting | North Inlet Marsh | | Paynes Prairie | | Probability of difference |
|---|---|---|---|---|---|
| | No. of pounces | Percent success | No. of pounces | Percent success | |
| Hook pounce | 20 | 25.0 | 203 | 7.9 | $\chi^2 = 6.3$, $P < 0.025$ |
| Hover pounce | 42 | 19.5 | 206 | 2.9 | $\chi^2 = 17.6$, $P < 0.0005$ |
| Straight pounce | 26 | 23.1 | 167 | 8.4 | $\chi^2 = 5.2$, $P < 0.025$ |
| Touch down | 66 | 0.0 | 94 | 2.1 | No test |
| Bird chase | 51 | 23.5 | 17 | 11.8 | $\chi^2 = 1.1$, $P > 0.20$ |
| All combined | 205 | 15.1 | 687 | 5.8 | $\chi^2 = 18.6$, $P < 0.0005$ |

TABLE 3. Prey taken by Northern Harriers wintering in North Inlet Marsh, South Carolina, and Paynes Prairie, Florida.

| Species | North Inlet Marsh | Paynes Prairie |
|---|---|---|
| Mammals | | |
| *Sigmodon hispidus* | 0 | 12 |
| Unidentified small mammal | 0 | 1 |
| Birds | | |
| *Anas discors* | 1 | 0 |
| *Porzana carolina* | 2 | 0 |
| *Rallus longirostris* | 3 | 0 |
| *Tringa* sp. | 1 | 0 |
| *Calidris alpina* | 1 | 0 |
| *Agelaius phoeniceus* | 2 | 0 |
| *Quiscalus major* | 1 | 0 |
| Emberizidae | 13 | 4 |
| Unidentified shorebird | 3 | 0 |
| Unidentified passerine | 4 | 0 |
| Reptiles | | |
| Unidentified snake | 0 | 1 |
| Unidentified prey | 0 | 22 |
| Total | 31 | 40 |

Prairie (85.8 g) were comparable. As a result, estimates of prey biomass captured by harriers in the two habitats were similar; harriers captured prey at a rate of 27 g/h of hunting at North Inlet Marsh and 23 g/h of hunting at Paynes Prairie.

## DISCUSSION

Northern Harriers wintering in South Carolina and Florida exhibited substantial differences in foraging behavior, hunting success, and diet but caught prey at similar rates. The ability of harriers to exploit different capture techniques in habitats that support different prey populations no doubt contributes to their widespread winter distribution. It is not known, however, if harriers develop specific habitat preferences and return to previously used wintering sites. Winter site fidelity has been documented for the American Kestrel (*Falco sparverius;* Mills 1976, Tabb 1977, Bolen and Derden 1980, Layne 1982), and it seems reasonable that wintering harriers that use a particular habitat type and prey base might return in subsequent winters to the same or similar areas. Conversely, harriers might not develop habitat preferences but rather might use a variety of habitats in winter depending on local prey availability. Our results, however, indicate that if harriers switch between salt and freshwater marshes, they would need to make significant changes in their foraging behavior and diet.

Our data show that habitat type and prey base influence the foraging behavior and hunting success of harriers. Harriers hunting for birds on North Inlet Marsh had higher success rates (15.1%) than those foraging primarily on cotton rats in Paynes Prairie (5.8%). This does not support the generalization that hunting success declines as increasingly mobile prey taxa are taken (Newton 1979, Temeles 1985). Prey mobility undoubtedly is an important influence on capture success by raptors and may account for much of the variation in capture success among raptors foraging in different trophic levels; however, habitat structure also is important in determining raptor hunting success (Baker and Brooks 1981). We found that avian prey from North Inlet Marsh were relatively vulnerable to harrier predation, as they often were flushed from isolated, floating wracks of detrital vegetation. Furthermore, the birds most commonly captured (rails and sparrows) were

TABLE 4. Capture rates of Northern Harriers wintering on North Inlet Marsh, South Carolina, and Paynes Prairie, Florida.

| | North Inlet Marsh | | | Paynes Prairie | | |
|---|---|---|---|---|---|---|
| Sex/age class | No. of captures | Captures/h of hunting | Captures/h of observation | No. of captures | Captures/h of hunting | Captures/h of observation |
| Adult male | 1 | 0.31 | 0.16 | 5 | 0.75 | 0.26 |
| Adult female | 21 | 1.04 | 0.32 | 19 | 1.05 | 0.27 |
| Juvenile | 5 | 0.55 | 0.20 | 11 | 1.20 | 0.30 |
| Brown bird[a] | 4 | 1.24 | 0.43 | 5 | 0.77 | 0.23 |
| Total | 31 | 0.87 | 0.29 | 40 | 0.99 | 0.27 |

[a] Includes adult females and juveniles of both sexes.

not highly maneuverable when flying from harriers, but rather exhibited rapid, linear flights to escape cover. These flight patterns also may have contributed to the success of harriers foraging in the salt marsh. On Paynes Prairie, cotton rats, which were concealed in their runways beneath tall stands of dense vegetation, appeared difficult to capture. Avian prey, which generally are considered the more mobile and elusive prey taxa (Newton 1979), were captured more easily on North Inlet Marsh than were small mammals on Paynes Prairie.

Most studies of raptor foraging behavior simply report the species' overall hunting success (see Temeles 1985 for review). Although several studies have evaluated hunting success in relation to prey taxa (Collopy 1973, Balgooyen 1976, Hector 1981, Shrubb 1982, Village 1983, Temeles 1985), all have been site specific. These reports support the generalization that increasingly mobile prey (i.e. birds vs. small mammals) are more difficult to capture. For several species, however, including American Kestrels (Jenkins 1970, Balgooyen 1976, Bohall and Collopy in press), Black-shouldered Kites (*Elanus caeruleus*; Bammann 1975, Warner and Rudd 1975, Tarboton 1978), and Peregrine Falcons (*Falco peregrinus*; Monneret 1973, Parker 1979, Treleaven 1980), studies have been conducted that show between-site differences in hunting success for similar prey taxa. These differences suggest that habitat effects, similar to those seen in our study, may occur with other species. Therefore, we suggest that studies designed to test the influence of different prey types on capture success do so within the same habitat.

Many raptors exhibit habitat segregation between sexes in winter (Hunt et al. 1975, Koplin 1973, Mills 1976, Newton 1979, Bildstein in press), a phenomenon that often is a part of discussions concerning sexual size dimorphism and diet (see Newton 1979 for review). Our results indicate that, for harriers at least, researchers need to consider the extent to which the habitat and prey base encountered by each sex modifies foraging behavior and hunting success before conclusions are made about inherent sexual differences in hunting success. For example, among species that exhibit winter habitat segregation between the sexes, what appears to be a sexual difference in hunting success may be largely a habitat or prey-base effect. Finally, our results emphasize the need for more comparative studies of raptor foraging behavior, particularly those that simultaneously document foraging behavior, hunting success, and diet in different habitats.

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