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BEHAVIOR OF MIGRATING RAPTORS: DIFFERENCES BETWEEN SPRING AND FALL

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ABSTRACT.—Forty percent of all raptors observed in spring migration at Cedar Grove, Wisconsin, were southbound (reversed). Northern Harriers (*Circus cyaneus*), Cooper's Hawks (*Accipiter cooperii*), and American Kestrels (*Falco sparverius*) comprised a larger proportion of the migrants in spring than in fall, presumably because they bred at that latitude and many were reorienting and searching for their breeding territories. Raptors migrating in spring attacked birds used as lures in traps more frequently, attacked larger species more frequently and culminated attacks by actually striking the lure more often in spring than in fall. Lure birds which could not flee or become immobile appear as easy prey for raptors. Prey may be scarcer and more experienced in spring than in fall and, thus, easy prey may be more attractive in spring.

Conducta predatoria de aves raptoras migrantes: diferencias entre primavera y otoño

EXTRACTO.—Durante la migración de primavera en Cedar Grove, Wisconsin, 40% de todas las aves rapaces observadas migraron hacia el sur (en sentido contrario). *Circus cyaneus, Accipiter cooperii* y *Falco sparverius* comprendieron la mayor proporción de migrantes durante la primavera comparada con la del otoño, debido a que, presumiblemente, ellos se reproducen en esa latitud y muchos estuvieron reorientándose y buscando sus territorios para su reproducción y cría. En la primavera, las rapaces migratorias atacaron con mayor frecuencia a las aves usadas como señuelo en trampas, ellas atacaron con más frecuencia a las especies más grandes y culminaron sus ataques golpeando efectivamente a los cebos más a menudo en primavera que en otoño. Las aves señuelo, las cuales no pudieron huir ni permanecer inmóbiles, fueron presa fácil para las rapaces. En la primavera, la presa puede ser más escasa y tener más experiencia que en el otoño, resultando por lo tanto que la presa fácil puede ser más atractiva en primavera.

When we first met the Hamerstroms, they were "strictly for the chickens." Dan was an aspiring falconer and Helmut a bird watcher. Hammy helped inspire us to more scientific pursuits and our fascination with raptors led us to start the Cedar Grove Ornithological Station. We spent much time at the Hamerstroms' in the early 1950s and their interests in raptors rekindled as ours developed. Fran and Hammy began visiting Cedar Grove in the mid 1950s and became more and more involved in our activities. Hammy's expertise in carpentry was much appreciated in the building of the station after a fire destroyed the original shanty in 1958. This paper draws upon data that Hammy helped gather, working in a structure he helped design and build.

Most species of raptors are opportunistic and alter their diet as the availability of prey changes. Prey are scarcer, more experienced, and more difficult to obtain in spring than in autumn because there is little or no reproduction in the winter. This paper explores the possibility that the prey preferences of three species of Falconiformes change over the winter and that the probability of attack on three sizes of avian prey might be different in spring migration than in fall migration.

METHODS

Observation and trapping of migrating hawks were conducted in both the springs and autumns of 1953–57 and 1962–65 at the Cedar Grove Ornithological Station in Sheboygan County, Wisconsin. A description of the area can be found in Mueller and Berger (1966), of the trapping methods in Bub (1991), and of the raptor migrations in Mueller and Berger (1961, 1969).

We used domestic pigeons (*Columba livia,* mass 350 g), European Starlings (*Sturnus vulgaris,* mass 80 g) and House Sparrows (*Passer domesticus,* mass 28 g) as lures. Hawks were trapped in bownets if they struck the lure (henceforth, "strikes") or in dho-gazas if they passed over the lure ("passes") or encountered the dho-gaza en route to the lure. In the latter event it is impossible to state whether

or not the raptor might have struck the lure and these hawks were deleted from analyses of strikes and passes. "Attacks" refer to birds that approached our lures closely enough to be captured in bownets or dho-gazas. Some birds approached closely but did not fly into a net or escaped. These events were not recorded consistently, particularly in the 1950s, and are not included in our analyses. Dho-gazas were down more frequently in spring than in fall because of high winds and this might slightly bias the data in favor of fewer passes and more strikes in spring. Pigeons were used as lures on two of our traps. The one used most frequently lacked dho-gazas and could capture birds only in a bownet. There were too few captures in the other trap to permit an analysis of strikes vs. passes and we thus limit these comparisons to attacks on starlings or sparrows.

Seasonal changes in the frequency of attacks on lure birds, in the ratio of attacks on pigeons to attacks on smaller lures and in the ratio of strikes to passes were interpreted as evidence of shifts in prey preference or motivation. We use mass of the captured hawk or falcon as an index of hunger. Birds were weighed in aluminum cylinders to the nearest gram on a triple-beam balance calibrated to 0.1 g.

We selected three species for analysis: Northern Harrier (*Circus cyaneus*), Cooper's Hawk (*Accipiter cooperii*), and American Kestrel (*Falco sparverius*). Together, they account for 50% of raptors observed, and almost 80% of raptors trapped in spring at Cedar Grove. The harrier preys on both birds and small mammals, but it is the latter that predominate when available. The Cooper's Hawk is primarily a specialist on birds, although mammals are also taken. The kestrel feeds on a variety of invertebrates and small vertebrates, but insects, primarily grasshoppers, are the most common prey in late summer and fall, until cold weather forces the birds to shift to a diet consisting of primarily small mammals (see Palmer 1988, or Johnsgard 1990 for a summary of studies of the diet of these species). The dietary habits of the three species leads to the following predictions: kestrels should show the greatest change in prey between fall and spring, harriers less, and there should be little or no change in Cooper's hawks.

Age and sex of the hawks observed but not caught was not consistently determined or recorded. There are possibly age and sex biases in the probability of capture and our data provide little information on the age or sex ratio of migrants. Determining the age of male kestrels is difficult in late fall and almost impossible in spring and we were also inconsistent in our determination of age in the 1950s. The small and possibly biased samples of aged kestrels were not amenable to statistical analysis and we thus divided the sample by sex only.

SYSTAT 5.1 for the MacIntosh (Wilkinson 1989) was used for statistical analysis. Unless otherwise stated, chi-square tests are of 2 × 2 contingency tables with one degree of freedom. Sample sizes differ slightly for the various comparisons because there were occasional omissions and errors in measurement or recording (the latter were deleted) and because some of the original field notes for 1953 have been lost, leaving only a summary of the data.

RESULTS

Five times as many hawks were observed in fall as in spring but only three times as many attacked lures and were trapped (Table 1). In spring, all three species attacked lures more frequently when southbound than northbound (Fig. 1). Southbound birds in spring attacked lures more frequently than fall migrants (almost all migrants in fall were southbound) but there was no statistically significant difference in the frequency of attacks between fall and northbound spring migrants (Fig. 1). Cooper's hawks and harriers attacked proportionally more pigeons than starlings and sparrows in spring than in fall (Fig. 2). There were no statistically significant differences between spring north- and southbound harriers and Cooper's hawks in the proportions of attacks on the three species of lures. No kestrel attacked a pigeon and too few attacked starlings to permit a statistical comparison with attacks on sparrows. More harriers and kestrels culminated their attacks by actually striking the lure bird in spring than in fall (Fig. 3). Most Cooper's hawks actually struck the lure and too few merely stooped over the lure to permit statistical comparison between seasons.

There was no consistent relationship between mean mass of captured raptors and season. Southbound males in spring were lighter than in fall in all three species but the difference is statistically significant in only two of five comparisons. Northbound males (Fig. 4–6) were lighter than fall migrants in four of five comparisons but none of the differences are statistically significant. In contrast, females were heavier in spring than in fall, both north- and southbound, in kestrels and Cooper's hawks, and significantly so in three of four comparisons in the latter species. However, female harriers conformed to the pattern shown in males and were lighter in spring than in fall in all of four comparisons, and significantly so in two comparisons. Interestingly, southbound raptors of both sexes of all three species were lighter than northbound in all but one of ten comparisons, and the difference is statistically significant in two cases.

Overall, female Cooper's attacked pigeons more frequently than males (Fig. 7), a difference to be expected because of the pronounced sexual dimorphism in size (Fig. 5). But harriers are also very dimorphic (Fig. 4) and there is no difference between the sexes in the frequency of attacks on pigeons (Fig. 7). There were significantly more immatures among southbound harriers than among northbound birds (Fig. 8). Adult harriers attacked pigeons more often than immatures, but there was no age difference in attacks on pigeons in Cooper's hawks (Fig. 7). Note

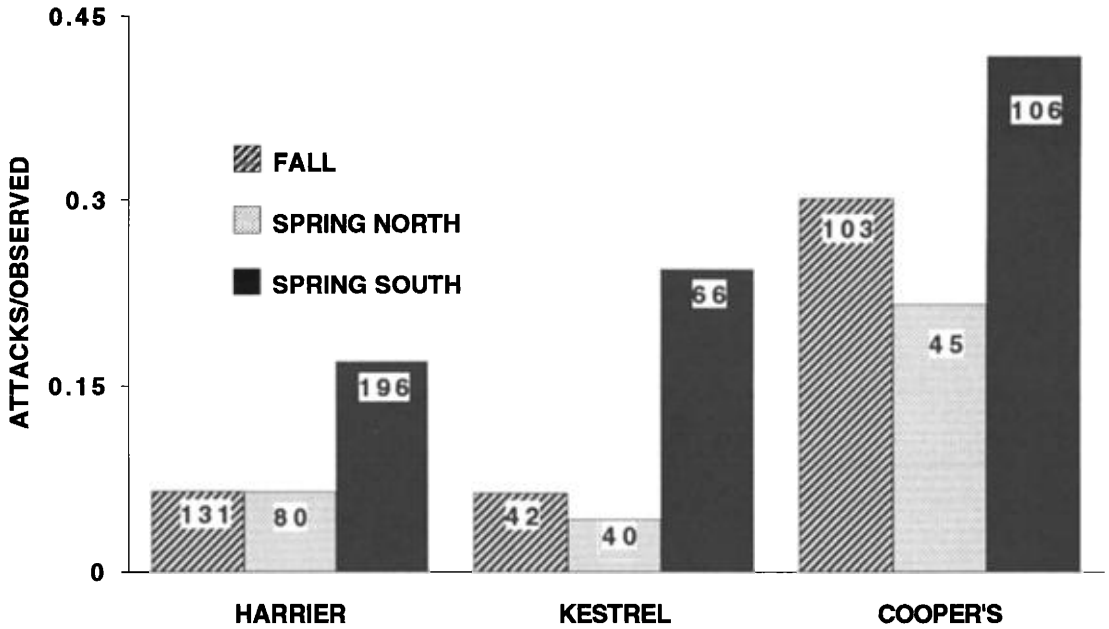

Figure 1. Proportion of raptors observed that attacked lures. The numbers indicate the number of attacks. Southbound birds in spring attacked more frequently than fall migrants (harrier, $\chi^2 = 71$, $P < 0.0001$; Cooper's, $\chi^2 = 4.11$, $P < 0.05$; kestrel, $\chi^2 = 46$, $P < 0.0001$). Southbound birds attacked more frequently than northbound birds (harrier, $\chi^2 = 53$, $P < 0.0001$; Cooper's, $\chi^2 = 11.1$, $P < 0.0009$; kestrel, $\chi^2 = 84$, $P < 0.0001$). No other differences within species are statistically significant ($P > 0.05$).

that the data in Fig. 7 are for spring only. Both species attack proportionately more pigeons in spring than in fall (Fig. 2) and this analysis had to be restricted to one season. Spring was chosen because too few adult harriers attacked pigeons in fall to permit statistical analysis (1 of 14 adults, 6 of 115 immatures).

DISCUSSION

Five times as many hawks were observed in fall at Cedar Grove as in spring but 40% of the spring migrants were southbound and probably more than a few of these were already counted going north. There are a variety of factors that might explain the differences between spring and fall in the number of migrant raptors observed. The shoreline of Lake Michigan acts as a leading line concentrating watershy raptors (Mueller and Berger 1967). Locally, the shoreline is oriented NNE-SSW, considerably more effective in concentrating south- than northbound migrants. Lake Michigan is very cold in spring and the air over it is cooled accordingly. A shallow layer of cold, dense air often extends inland, often for several hundred meters and occasionally for several kilometers, persisting even in the face of a moderately strong westerly wind if the air inland is warm. The warm air slides up and over the cold air, creating a line of updrafts. These updrafts can be utilized by raptors and would concentrate them some distance inland and often beyond the view of our observation blind. On a larger scale, the shoreline of Lake Michigan is much better oriented for concentrating souththan northbound migrants. The average orientation of the shoreline to the outskirts of the Milwaukee metropolitan area, 34 km away, is 15° west of south. A line drawn south of Cedar Grove extends over Lake Michigan for 52 km before making a brief landfall north of Racine, Wisconsin, the next brief landfall is near Zion, Illinois, 118 km south, and continuous passage overland is not attained until the metropolitan Chicago area, 150 km south. The southern end of Lake Michigan is not much farther south. The large cities of Chicago, Milwaukee and the considerable urban development between them further inhibit the concentrating effects of the shoreline on migration (Mueller and Berger 1967). In

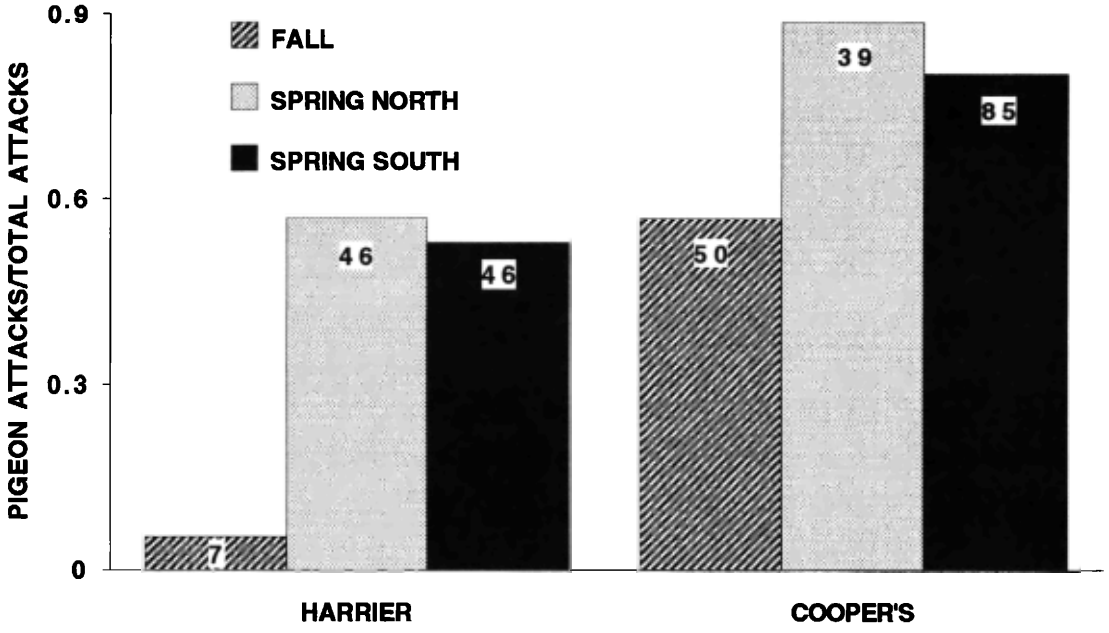

Figure 2. Attacks on pigeons as a proportion of all attacks on lures. The numbers indicate the number of attacks on pigeons. Raptors attacked pigeons more frequently in spring than in fall (harriers: northbound, $\chi^2 = 78$, $P < 0.0001$; southbound, $\chi^2 = 70$, $P < 0.001$. Coopers': northbound, $\chi^2 = 13.5$, $P < 0.003$; southbound, $\chi^2 = 12.4$, $P < 0.005$). No kestrel attacked a pigeon.

contrast, a line drawn north from Cedar Grove never again strikes the main body of Lake Michigan, and variously effective leading lines of Lake Michigan and Green Bay reach to the upper peninsula of Michigan 240 km to the north.

The number of hawks observed at Cedar Grove is only an index of the number of migrants passing through the region. The weather, particularly wind direction, strongly influences the concentration of migrants along the lakeshore (Mueller and Berger 1961). Hawks southbound in spring have previously migrated north that season and may have been counted at Cedar Grove as northbound migrants. Indeed, it is possible that some migrants were counted several times in one season but this is unlikely to occur often because conditions suitable for bringing migrants over the station occur only sporadically. Southbound birds are considerably more likely to occur at Cedar Grove than northbound birds because of the greater effectiveness of leading lines to the north. It is thus difficult to compare the numbers of hawks seen in fall and spring. The best comparison is obviously between northbound spring birds and (southbound) fall birds but the former is obviously an underestimate, or the latter an overestimate, of the number of hawks passing through the region because of the differences in the leading lines in the two directions.

In absolute numbers, more harriers and Cooper's hawks were seen in fall than were seen northbound in spring, but almost half again as many kestrels were seen northbound in spring as southbound in fall. A migratory direction west of south in fall and east of north in the spring would result in more kestrels being concentrated on the western shore of Lake Michigan in spring than in fall. If this is true, we might expect that band recoveries of kestrels to the south of Cedar Grove should be concentrated to the west. A cursory examination fails to reveal an obvious pattern but final judgment awaits a detailed examination. Although the numbers of harriers and Cooper's hawks observed northbound at Cedar Grove in spring do not exceed the numbers seen in fall, it is probable that they also are present along the lakeshore in spring in excessive numbers and require an explanation similar to what we have tentatively proposed for kestrels.

Broad-winged Hawks (*Buteo platypterus*) and Sharp-shinned Hawks (*A. striatus*) are the most com-

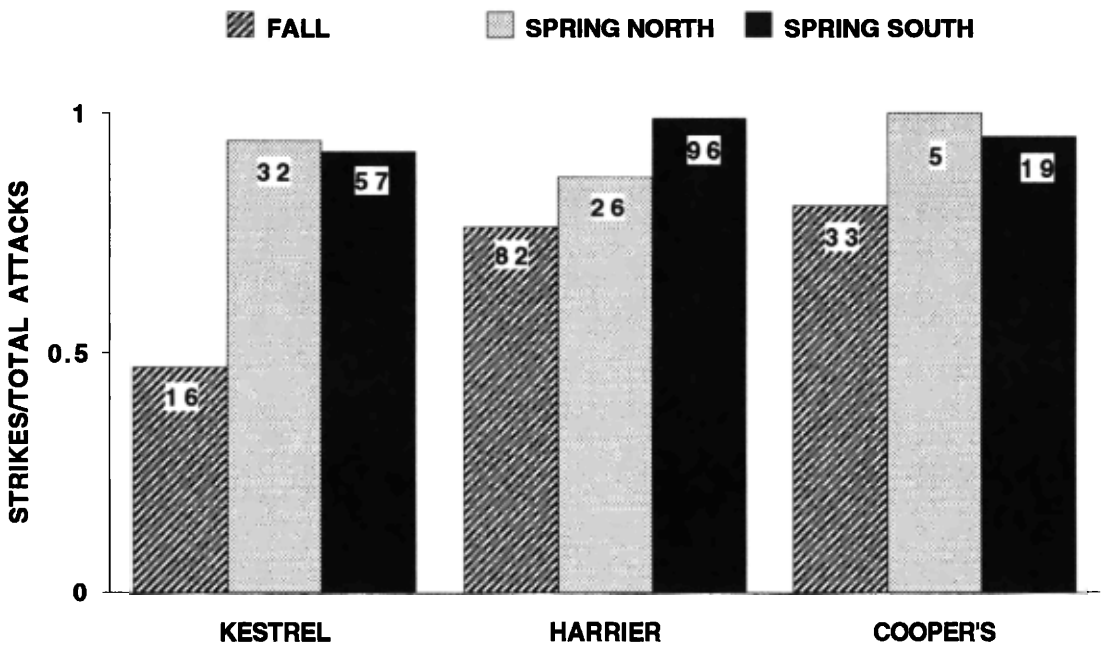

Figure 3. Proportion of attacks that culminated in strikes instead of passes over starlings or sparrows. The numbers indicate the number of strikes. Raptors struck prey more frequently in spring than in fall (kestrels: northbound, $\chi^2 = 18.7$, $P < 0.001$; southbound, $\chi^2 = 24.3$, $P < 0.001$. Harriers: southbound, $\chi^2 = 24$, $P < 0.001$; northbound, n.s. Most Cooper's hawks struck the lures and too few passed to permit statistical analysis).

mon raptors in fall at Cedar Grove, constituting as much as 84% of the migrants observed (Mueller and Berger 1961) but are much less common in spring, constituting less than 25% of the raptors seen. All but a few individuals of these two forest inhabiting species nest to the north of the latitude of Cedar Grove (43°40'N). Many breed to the northwest and may migrate to the southeast in fall to avoid the treeless plains, a migratory direction that would enhance their chances of encountering the western shore of Lake Michigan. A complementary migratory di-

Table 1. Migrant Falconiformes observed and trapped at Cedar Grove, Wisconsin.

	Number Observed (% Southbound)		Number Trapped	
Species	Fall	Spring	Fall	Spring
All	48 419	9366 (40.6)	2539	851
Harrier	2042	2710 (47.9)	131	328
Cooper's	342	597 (54.9)	103	187
Kestrel	806	1453 (22.0)	42	157

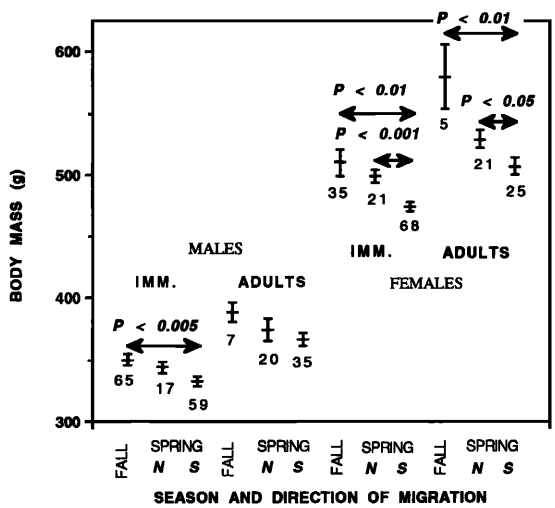

Figure 4. Body mass of Northern Harriers. The bars indicate the mean ± 1 SE. The numbers indicate the sample size. The arrows connect samples for the indicated statistical significance. Statistical differences were determined by t-test.

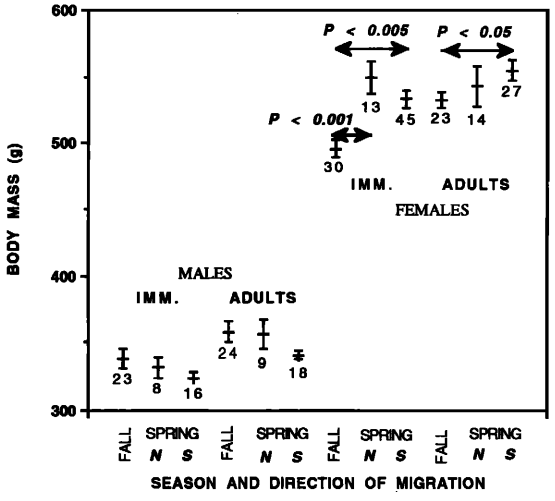

Figure 5. Body mass of Cooper's Hawks. Conventions as in Fig. 4.

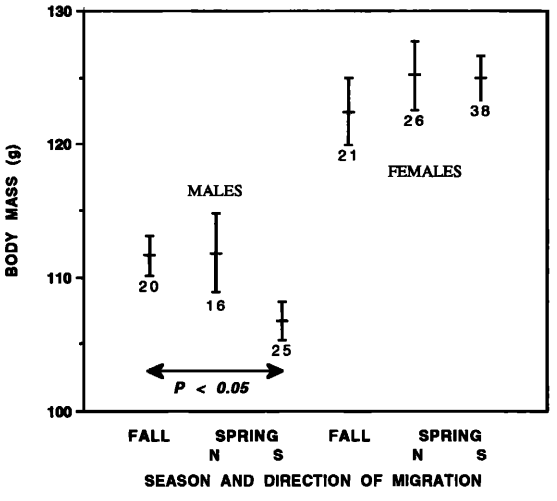

Figure 6. Body mass of American Kestrels. Conventions as in Fig. 4.

rection of northwest in spring would lead them away from the western shore.

Unlike the broad-wing and sharp-shin, Cooper's Hawks, kestrels and harriers breed commonly both north and south of the latitude of Cedar Grove (Palmer 1988, Robbins 1991). Mueller and Berger (1969) have suggested that many of the southbound migrants at Cedar Grove in spring are birds that

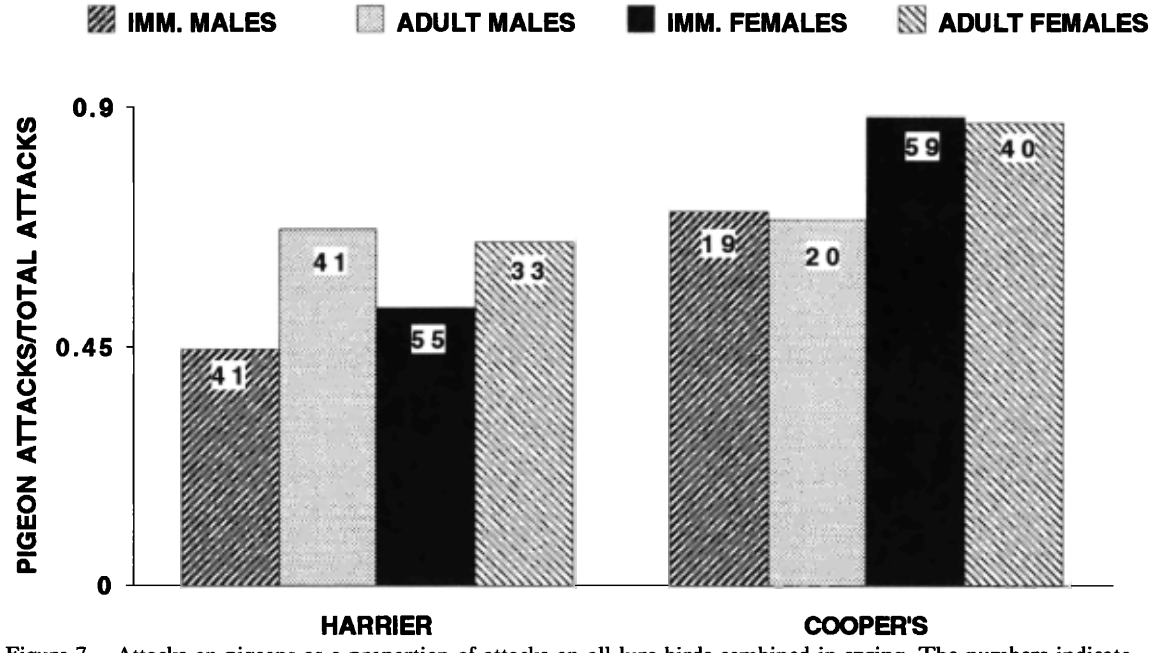

Figure 7. Attacks on pigeons as a proportion of attacks on all lure birds combined in spring. The numbers indicate the number of attacks on pigeons. Female Cooper's Hawks (adults and immatures combined) attacked pigeons more frequently than males ($\chi^2 = 8.86$, $P < 0.003$). Adult Northern Harriers attacked (sexes combined) pigeons more frequently than immatures ($\chi^2 = 8.48$, $P < 0.004$).

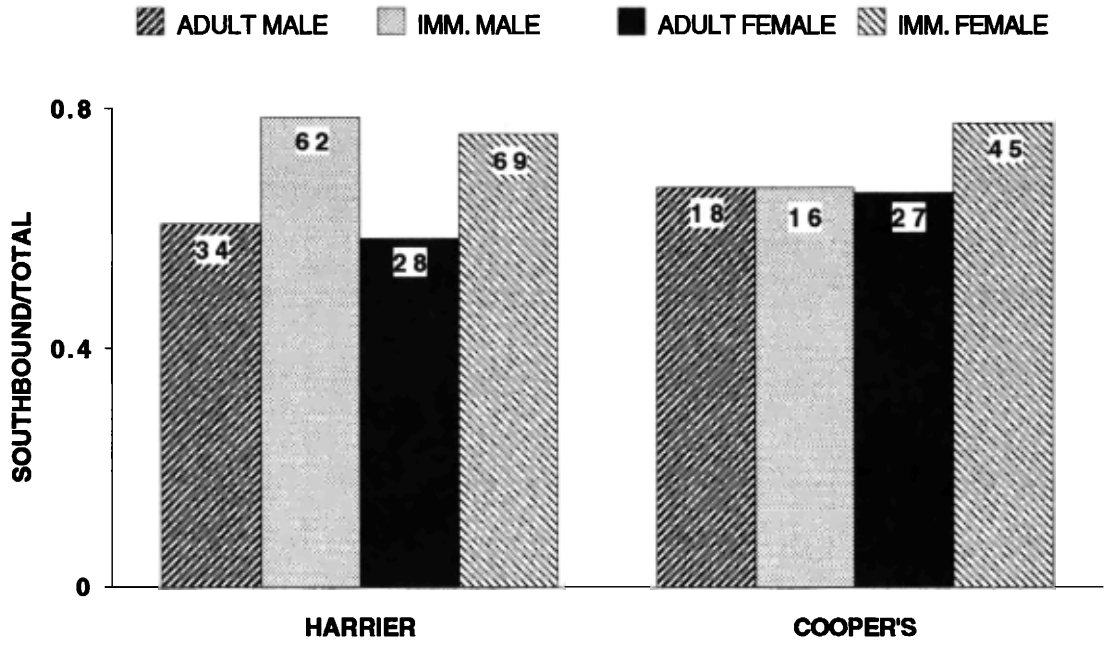

Figure 8. Southbound migrants trapped as a proportion of all spring migrants trapped. The numbers indicate the number of southbound birds trapped. More immature than adult Northern Harriers (sexes combined) were captured migrating south in spring ($\chi^2 = 9.43$, $P < 0.003$).

are searching for, or reorienting, to their summer territories to the south or east of Cedar Grove after migrating too far west or north. Perhaps some of the northbound birds are reorienting to the east as well after having reached the approximate latitude of their summer home. If the navigation of hawks is as crude as Mueller and Berger (1969) have suggested, individuals of species that breed mainly to the north of Cedar Grove (such as broad-wings and sharp-shins) would still be wandering north and are less likely to be concentrated along the lake shore than reorienting individuals.

About half of the harriers and Cooper's hawks, but only one of five kestrels observed in spring are southbound (Table 1). Harriers and Cooper's hawks breed only uncommonly in the immature plumage but most kestrels breed in their first year (Meng and Rosenfield 1988, Bildstein and Gollop 1988, Henny 1972). Thus, more harriers and Cooper's hawks are non-breeders and may be wandering rather than homing to a specific breeding area, and are more likely to be southbound in spring than kestrels.

A greater proportion of the harriers captured while migrating south in spring were immatures than of those migrating north. It is unlikely that the direction of migration affects the tendency to attack prey differently in adults and immatures; the most probable explanation is that immatures are more likely to reverse their northward migration than adults. There are no differences between the age ratios of north- and southbound Cooper's and it is not clear why the two species differ in this respect. Both breed at, and north and south of, the latitude of the station, but the Cooper's hawk is much closer to the northern limits of its breeding range than the harrier (Palmer 1988). All but a few adult Cooper's in their second year of life are embarking on their first breeding season and searching for a place to breed. Perhaps these first-time breeders are likely to migrate too far north, into areas which are only sparsely populated by the species and then reverse their direction and occur as southbound migrants at Cedar Grove. As noted previously, harriers and Cooper's hawks breed at about the same time in Wisconsin. Both species breed only uncommonly in the immature plumage, but the variance in the age ratio is higher in harriers, with more immatures breeding when vole populations are high (Hamerstrom 1988). Local popula-

tions of harriers fluctuate considerably in response to vole populations and breeding site fidelity appears to be lower in harriers than in Cooper's (cf., Hamerstrom 1986, and Moore and Henny 1984). We might thus expect young harriers to wander and search for a possible breeding locality more than Cooper's hawks. Young harriers return to their birthplace to breed less frequently than Cooper's hawks (cf., Hamerstrom 1986, Rosenfield and Bielefeldt 1992). A bird wandering eastward is more likely to pass over Cedar Grove if it turns south rather than north because of the greater effectiveness of the leading line. Immature harriers may be more likely to turn south than birds that have bred previously when they encounter the lake shore because more of them are wandering rather than attempting to return to a breeding area to the north of Cedar Grove.

In spring, southbound harriers, Cooper's and kestrels attacked our lure birds more frequently than northbound migrants. Our blind and traps are permanent structures situated, oriented and designed for the capture of southbound migrants in fall. Our lure birds must be manipulated by the trapper to be effective in attracting raptors to our traps. Northbound migrants usually are not observed from our blind until they are overhead or off to the east or west and, at best, there is very little time to operate before the birds are past and unlikely to see our lures. On some occasions we put an auxiliary observer in a small blind to the north of our traps to watch for northbound hawks and signal the trapper in the main blind. There are trees immediately to the south of our blind and the view of the auxiliary observer is far from optimal. The signaling system was also crude: variously a whistle, an electric buzzer and an old telephone. These efforts did not seem to affect the probabilities of our capturing northbound migrants consistently. Indeed, we suspect, but cannot prove, that northbound migrants would be more difficult to trap than southbound migrants even if we built a blind and traps specifically for them. Northbound migrants may be less hungry or more motivated to migrate than southbound birds. Regardless of these possibilities, the probability of capture is biased in favor of southbound birds and most comparisons between spring and fall can only be made properly among southbound birds.

In all three species, southbound migrants in spring attacked prey more frequently than fall migrants. Of the raptors attracted by our lures, more struck the lure when southbound in spring than in fall. Cooper's and harriers attacked larger prey (pigeons) more often in spring than in fall. Three possible explanations for these seasonal changes are: 1) raptors are hungrier in spring; 2) prey are scarcer in spring, more difficult to capture and raptors must avail themselves of almost every opportunity to capture prey; and 3) the specific searching images (Tinbergen 1960, Mueller 1971, 1987) of raptors change over the winter in response to changing availabilities of prey types. These hypotheses are not mutually exclusive and there is no reason each must apply to all three species. Harriers, and particularly kestrels, may change their search image over the winter but this is clearly not the case with Cooper's hawks which prey largely on birds year-round. Hunger is also an inadequate explanation if the body mass of raptors is an unequivocal measure of appetite. Female kestrels and female Cooper's were heavier in spring than in fall (the difference is statistically significant in the latter). Yet females of both these species do not differ from males in attacking more lure birds in spring than in fall. Females may put on more fat in spring than males in preparation for breeding. This is true of the European Sparrowhawk (*A. nisus*; Newton 1986) and the Eurasian Kestrel (*F. tinnunculus*; Village 1990). A female thus might be as hungry as a male in spring even though she is fatter than the male. However, female harriers are significantly lighter, not heavier, in spring than in fall (Fig. 4), and yet they breed at approximately the same time as Cooper's and kestrels (Robbins 1991). Further inconsistencies are that male harriers and kestrels all weigh significantly less in spring than in fall and Cooper's show the same trend. Male European Sparrowhawks are heavier in spring, possibly significantly so, and Eurasian Kestrels also appear to be slightly heavier in spring than in fall. Southbound hawks of all three species attack lures more often than northbound hawks and are lighter in nine of ten comparisons and the difference is statistically significant in two cases. This nearly consistent relationship further highlights the lack of consistency in differences between fall and spring.

The remaining hypothesis, that raptors must avail themselves of opportunities of capturing prey more frequently in spring than in fall because prey is scarcer has the further virtue in being the most parsimonious of the three. Our lures are obviously attractive to raptors since we capture a reasonable proportion of the birds that we observe (Table 1, Fig. 1). One can see more attacks on birds at a hawk

trapping station in a day or two than in a lifetime of watching migrating hawks. Our lures cannot use the predator evasion tactics of immobility to avoid detection or fleeing to avoid attack. Birds that fail to use evasive tactics in the presence of a raptor must be unusual in nature and particularly rare in spring because young of the previous breeding season have had at least a half-year's experience avoiding predation and no new inexperienced young have yet appeared. Our lures should thus be more attractive in spring.

The fourfold increase in frequency of attacks on lure birds between fall and spring by kestrels can be interpreted as a switch in the specific searching image of many individuals from grasshoppers to vertebrates. On the other hand, the 1.6 fold increase in Cooper's hawks is also considerable and a change in specific searching image is not a likely explanation.

It is not surprising that female Cooper's hawks attack larger prey (pigeons) more frequently than males; females weigh about 1.5–1.6 times as much as males. However, harriers show no difference between the sexes in the frequency of attacks on pigeons even though harriers are essentially as dimorphic as Cooper's: female harriers weigh about 1.4–1.5 times as much as males (Fig. 4). Curiously, adult harriers attack pigeons more frequently than immatures but there is no such age difference in Cooper's hawks even though the age dimorphism is similar in the two species (Fig. 5, adult mass is 1.1 times that of immatures). In contrast, Mueller and Berger (1970) found that immature Sharp-shinned Hawks attacked pigeons during fall migration more frequently than adults and attributed the excessive attacks on inappropriately large prey to the relative inexperience of the young hawks. Too few harriers attack pigeons in fall for a statistical test and Fig. 7 is based on spring migrants. In spring, immature harriers have had more than 6 mo of experience but the greater experience of adults with large prey apparently is the reason adults attack pigeons more frequently. Most harriers strike the pigeons they attack (86% in fall and 99% in spring) but in 113 attacks on pigeons no sharp-shin actually struck the lure (Mueller and Berger 1970). It is unlikely that experience leads to frequent attacks on larger prey in one species and fewer in another species. We suggest that adult harriers attack pigeons more frequently than immatures because they have had successful experience with large prey. Pigeons are more than twice as large as female sharp-shins, and more than three times as large as male sharp-shins and are clearly excessively large prey for this species. We further suggest that the attacks on pigeons by sharp-shins are not mistaken predatory attempts on inappropriately large prey, but instead are a form of play behavior. Ratcliffe (1980), Treleaven (1980), Brown (1976), and Mueller and Meyer (1985) have noted that raptors often pursue prey without intent of capture. Young mammals exhibit play behavior much more frequently than adults and we might expect the same to be true of hawks. Mueller (1974) described some play behaviors in young hand-reared kestrels; play behavior in these birds decreased with age.

The explanations offered in this paper should be regarded as suggestions for further research rather than definitive answers to the interesting questions raised by the differences in the behavior of raptors between spring and fall migration.

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