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DIFFERENTIAL AUTUMN MIGRATION OF SHARP-SHINNED AND COOPER'S HAWKS IN WESTERN NORTH AMERICA¹

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Abstract. Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) showed differential migration timing during autumn migration in New Mexico and Nevada. Age-sex classes passed through both sites in this order: juvenile females, juvenile males, adult females, and adult males. We compared the magnitude of differential migration timing in these two species. The number of days separating mean passage dates of age classes (juvenile and adult) was greater for Sharp-shinned Hawks than for Cooper's Hawks. The number of days separating the mean passage dates of sex classes was mostly similar between the two species. In the Manzano Mountains of New Mexico, however, adult male and female Sharp-shinned Hawks were more separated than adult male and female Cooper's Hawks. In Sharp-shinned and Cooper's Hawks, it seems likely that differences in rate of travel between males and females may best explain sex-specific differential migration timing and that foraging efficiency (i.e., hunting skill level) may best explain age-specific differential migration timing.

Key words: *Accipiter cooperii*, *Accipiter striatus*, Cooper's Hawks, differential migration, foraging efficiency, Sharp-shinned Hawks.

Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks (*A. cooperii*) show differential migration timing at many locations throughout North America (Broun 1949, Mueller and Berger 1967, Devereux et al. 1985). Although there is considerable overlap, juveniles of these species precede adults, and females precede males past stationary observation sites (Rosenfield and Evans 1980, Hoffman 1985). The passage order shown by Sharp-shinned and Cooper's Hawks differs from that predicted by some prominent theories of differential migration, such as the social dominance (Gauthreaux 1982) and body size hypotheses (Kerlinger 1989), thus requiring the examination of other hypotheses. Temporal separation of age-sex classes during migration may arise from differences in onset or rate of migration among age-sex classes (Woodrey and Chandler 1997). We have found no literature describing age-sex class differences in onset or rate of migration for Sharp-shinned or Cooper's Hawks. Therefore, it is still unclear which process causes timing differences in these species.

Woodrey and Chandler (1997) suggested that comparing the magnitude of differential migration timing between species might create opportunities for examining hypotheses that explain this phenomenon. We follow their suggestion and compare the magnitude of differential migration shown by Sharp-shinned and Cooper's Hawks and discuss possible explanations for differential migration timing by age and sex for these two species.

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TABLE 1. Least square mean (LSM) capture dates and total sample sizes for age-sex classes of Sharp-shinned and Cooper's Hawks captured in the Manzano and Goshute Mountains, 1992–1996.

	Juvenile female		Juvenile male		Adult female		Adult male	
	LSM	<i>n</i>	LSM	<i>n</i>	LSM	<i>n</i>	LSM	<i>n</i>
Sharp-shinned Hawk								
Manzanos	22 Sept	818	25 Sept	760	3 Oct	759	8 Oct	455
Goshute	14 Sept	3,192	18 Sept	3,819	30 Sept	1,735	6 Oct	1,416
Cooper's Hawk								
Manzanos	22 Sept	403	25 Sept	395	26 Sept	565	29 Sept	465
Goshutes	15 Sept	1,279	20 Sept	1,186	21 Sept	1,640	26 Sept	854

METHODS

STUDY AREAS

The Manzano Mountains research site is in the Manzano Wilderness Area of the Cibola National Forest, Mountainair Ranger District, in central New Mexico (34°42'N, 106°24'W), approximately 56 km south-southeast of Albuquerque. The range forms a ridge 55 km long and is bordered by the Rio Grande Rift Valley to the west and the Estancia Valley to the east. Southbound migrants probably follow ridges in the Sangre de Cristo, Jemez, and Sandia Mountains into the Manzano Mountains. The west side of the range features steep terrain, and the west and east slopes contain a variety of forest, scrub, and meadow communities. Three banding stations are situated near Capilla Peak, at an average elevation of 2,730 m.

The Goshute Mountains research site is in the Goshutes Wilderness Study Area managed by the Bureau of Land Management, Elko District, in northeastern Nevada (40°25'N, 114°02'W), approximately 40 km southwest of Wendover. Five banding stations are situated about 8 km south of Goshute Peak, at an average elevation of 2,695 m. The Goshute site is described in more detail in Hoffman (1985).

FIELD METHODS

We captured hawks from mid August through late October in the Goshutes, and from early September through late October in the Manzanos. We took measurements and banded all birds prior to release. Species and sex identifications followed Hoffman et al. (1990). We aged birds using criteria established by Mueller et al. (1979, 1981) and present data for two general age classes: juvenile and adult. Juvenile birds were less than 1 year old and in juvenile plumage; adult birds were greater than 1 year old and in basic plumage.

We used banding data instead of count data because of the difficulty of reliably discriminating the sex of accipiters in flight. Birds may differ by age and sex in their susceptibility to capture, indicating that, for each age-sex cohort, the captured sample may not reflect a constant proportion of the flight. However, potential biases introduced by using banding data should only affect the magnitude of the sample and should be random with respect to the date of capture. Thus, banding data should be valid when used in studies of migration seasonality.

DATA ANALYSIS

We compiled data collected at both sites from 1992 through 1996. We conducted site-specific analyses with SYSTAT (SPSS Inc. 1997), using 4-way factorial analysis of variance (ANOVA) to determine the effect of species, age, sex, and year on passage date. We deemed a difference in the magnitude of differential migration shown by Sharp-shinned and Cooper's Hawks significant if species-by-age or species-by-sex interaction terms were significant ($P \leq 0.05$). To understand the nature of significant differences in the magnitude of Sharp-shinned and Cooper's Hawk differential migration, we looked at the least square mean capture dates for each age-sex class. We compared Sharp-shinned and Cooper's Hawks by the number of days (averaged over the five years of the study) separating the mean passage dates of each age-sex class.

RESULTS

Mean capture dates indicate that both species at both sites showed differential migration timing, and that age-sex classes passed the sites as follows: juvenile females, juvenile males, adult females, adult males (Table 1). This is the same sequence reported by Rosenfield and Evans (1980) for Sharp-shinned Hawks and by Hoffman (1985) for Cooper's Hawks. However, juvenile male Cooper's Hawks passed through both sites only one day ahead of adult female Cooper's Hawks (Table 1).

Analysis of variance revealed that passage date differed significantly ($P < 0.05$) by species, age, sex, and year in both the Manzanos and the Goshutes. At both sites, as indicated by least square means, Sharp-shinned Hawks came through later than Cooper's Hawks, adults flew later than juveniles, and males flew later than females. Species-by-age interactions were significant at both sites (Manzanos, $F_{1,4580} = 146.9$, $P < 0.001$; Goshutes, $F_{1,15081} = 844.6$, $P < 0.001$). The number of days separating mean passage dates of juveniles and adults was greater in Sharp-shinned than in Cooper's Hawks (Fig. 1A). The species-by-sex interaction was significant only in the Manzanos ($F_{1,4580} = 4.1$, $P < 0.05$), where the number of days separating adult males and adult females was greater for Sharp-shinned Hawks than for Cooper's Hawks. Otherwise, the number of days separating mean passage dates of males and females was similar between species (Fig. 1B). The significant species-by-year, age-by-year, and

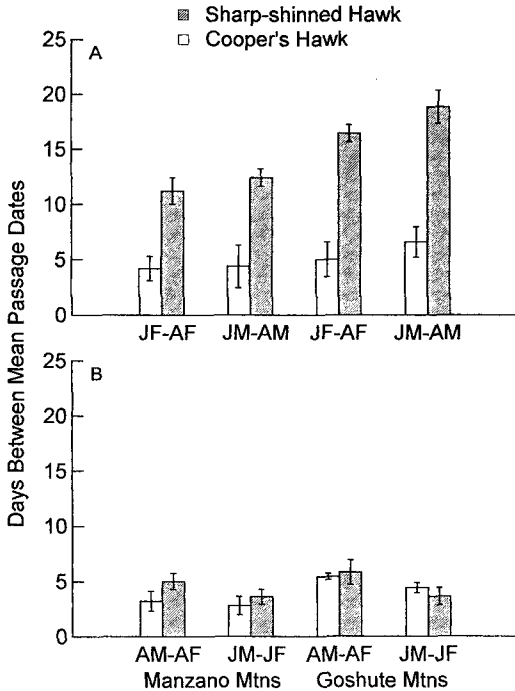


FIGURE 1. Mean (\pm SE) number of days separating mean passage dates of (A) age classes and (B) sex classes of Sharp-shinned and Cooper's Hawks captured in the Manzano and Goshute Mountains, averaged over the five years of the study. JF-AF refers to a comparison of juvenile females and adult females, JM-AM juvenile males and adult males, AM-AF adult males and adult females, JM-JF juvenile males and juvenile females.

sex-by-year interactions indicate that throughout the five years of the study, the separations of species, ages, and sexes varied in magnitude (except that sex separation in the Manzanos did not vary by year). The age-by-sex interaction was significant in the Goshutes only, where separation of sexes overall was slightly greater for adults than juveniles ($F_{1,15081} = 19, P < 0.001$).

Only two 3-way interactions were significant, both in the Goshutes. The species-by-age-by-year ($F_{4,15081} = 8.0, P < 0.001$) and age-by-sex-by-year ($F_{4,15081} = 5.0, P = 0.001$) interactions indicate that the way passage dates of age classes depended on species and sex varied by year. Examination of the least square means showed that the general pattern of the species-by-age and age-by-sex interactions held true and that only minor variations in passage date existed between years. The species-by-sex-by-year interaction was nearly significant, indicating that male and female Cooper's Hawks (summed over both age classes) may have preceded male and female Sharp-shinned Hawks to differing degrees each year.

DISCUSSION

Rosenfield and Evans (1980) proposed that differences in foraging efficiency could explain differences in the

onset of migration and the subsequent age-specific differential migration timing in Sharp-shinned Hawks. They suggested that juvenile birds are less efficient hunters than adults because of their inexperience, leading to differences in ability to tolerate declining prey availability in the fall. Therefore, juvenile birds would be expected to migrate before adults.

Assuming that foraging efficiency differences exist between adults and juveniles, we suggest that there are two reasons why we found that Sharp-shinned Hawks showed a greater magnitude of age-specific differential migration timing than Cooper's Hawks. First, juvenile and adult Sharp-shinned Hawks are farther apart in their ability to tolerate declining prey abundances than are juvenile and adult Cooper's Hawk. We suspect that this is not true, given their similar shapes and methods of hunting, but we have no way of evaluating this possibility.

Second, Sharp-shinned Hawks may experience more gradual prey declines than Cooper's Hawks. Differences in foraging ecology between these species may be important in determining the rate of decline in prey availability. Sharp-shinned Hawks take a higher proportion of birds than Cooper's Hawks (Johnsgard 1990, Rosenfield and Bielefeldt 1993). Although a large portion of the Sharp-shinned Hawk prey base leaves their breeding range during the fall, there may still be adequate bird prey throughout much of the fall migration period. The presence of nonmigrating, stopping-over, or wintering passerines in the Sharp-shinned Hawk breeding range and along migratory corridors could cause levels of prey to remain adequate for adults long after they became inadequate for juveniles. Although a large portion of the Cooper's Hawk prey base does not migrate, much of the mammal prey base enters hibernation or becomes buried by snow and leaf litter. Thus, Cooper's Hawks might experience rapid declines in prey availability when fall sets in. Adult Cooper's Hawks would thus tend to migrate shortly after juveniles, which was the case in our study.

In the Manzanos only, passage dates of adult males and females were more separated in Sharp-shinned than in Cooper's Hawks (Fig. 1B). Otherwise, males and females of both species were separated in migration timing by a comparable number of days. Rosenfield and Evans (1980) suggested that differences in prey choice because of sexual size-dimorphism in Sharp-shinned Hawks could cause differences in departure date and thus sex-specific differential migration timing. Males, at least in some localities, take smaller prey items than females (Snyder and Wiley 1976). Rosenfield and Evans (1980) thus reasoned that the smaller males have greater access to prey because there could be greater biomass in the smaller prey classes than in the larger, allowing males to depart later. This hypothesis rests on the assumption that autumn passerine migration does not affect size-specific abundance of passerines in the fall. On the other hand, females could depart on migration earlier than males if larger passerine prey species initiated migration earlier than smaller species.

An alternative explanation for sex-specific differential migration timing is that females may depart earlier than males because they may finish molting before

males (Smallwood 1988, Kjellén 1992). Females are known to initiate molt before males in both Sharp-shinned and Cooper's Hawks (Henny et al 1985), but it is unclear whether they actually complete the process before males. Both sexes of each species are regularly trapped during migration at the Goshutes and Manzanos with signs of ongoing or interrupted molt (pers. observ.). This observation indicates that neither sex needs to finish molt before initiating migration. However, an analysis of molt completion in accipiters might reveal a relationship between passage date and degree of molt completion. Even if molting influenced onset of migration in adults, however, it could not explain the temporal separation of sexes in non-molting juveniles.

Two alternatives based on the rate of migration seem more plausible. First, the sexes may migrate at different rates. Large birds fly faster than smaller birds (Calder 1984). Using equations that model the mechanics of flapping flight (Pennycuik 1989, 1997), we calculated the maximum range velocity for adult Sharp-shinned and Cooper's Hawks. Optimal velocities are predicted to be greater for females than for males in both species (Sharp-shinned Hawk, 19.0 and 17.5 m sec⁻¹, respectively; Cooper's Hawk, 22.9 and 21.2 m sec⁻¹, respectively). Females may thus progress faster than most males during migration, which would result in earlier passage dates for females at monitoring sites. We might predict that sex-specific differential migration timing at more southerly sites such as the Manzanos would be greater than at northern sites such as the Goshutes, but it is clear that this is not true in our study (Fig. 1B). However, the Goshutes and Manzanos monitoring sites do not sample the same populations (unpubl. banding data). Looking at such a comparison between two sites that sample the same populations might prove more informative.

Another possible explanation based on rate of travel is that males may spend less time per day in migratory flight than females. Because males are smaller and require more energy for flight and general maintenance than the larger females (Calder 1984), they may need to spend more time hunting per day than females. Such a phenomenon may be operating in tandem with slower flight speeds to cause males to pass through monitoring sites later than females.

Significant annual variation in the passage dates of these species suggests that the factors determining the onset or rate of migration also vary. Factors with significant annual variation, such as weather and prey availability, likely play an important role in determining either the onset or rate of migration in these species. However, it is beyond the scope of this paper to tease apart the relative influence of annual weather and prey abundance patterns on passage date or differential migration of these species.

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Goshutes project came from the U.S. Geological Survey, Biological Resources Division; U.S. Bureau of Land Management, Elko District; U.S. Fish and Wildlife Service, Region 1; Utah National Guard; and corporate sponsors, especially Barrick Goldstrike Mines, Coeur Rochester Mine, Echo Bay Management Corporation, Newmont Gold, and Placer-Dome U.S., Inc. A generous donation from Kay Millar and Dawn Sebesta helped support the preparation of this manuscript. We thank William DeRagon, James Gessaman, Kay Millar, Jessica Jewell, Jeff Smith, Kim Sullivan, and two anonymous persons for reviewing and commenting on this manuscript.

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FACULTATIVE COMMUNAL BROOD REARING IN CALIFORNIA QUAIL¹

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Abstract. We examined communal brooding in California Quail *Callipepla californica*. Most broods are reared by their parents alone, but 23 of 195 (12%) broods combined and were reared communally by all their living parents. A 26% greater fledgling rate of communally reared chicks was not statistically significant. Parents of communal broods lived significantly longer (3.1 years) than parents of single broods (1.9 years) and hatched significantly more young (36.3 vs. 15.7 young) during their lifetimes. Those that raised their first surviving brood communally were significantly (2.8 times) more likely to hatch a brood the following year. Communal brood fathers sentinelled significantly less and ate significantly more. We do not know whether parents initiated brood merging, thereby increasing their direct fitness, or the young initiated brood merging, thereby increasing their inclusive fitness. Broods combined only when they were hatched from nearby nests. Communal brood rearing may be constrained by the absence of pre-hatch contact between the parents, or by the limited mobility of young chicks.

Key words: *California Quail*, *Callipepla californica*, communal broods, fitness.

Both cooperative parental care and nuclear family care occur in several species of birds. Most are altricial species nesting in a single nest (e.g., Stacey and Koenig 1990, Armstrong and Juritz 1996). California Quail (*Callipepla californica*) are not known to nest together, but we and J. Calkins (pers. comm.) have observed

broods merging posthatch and being reared together. Brown et al. (1998) report merged broods in Gambel's Quail (*Callipepla gambelii*).

Cooperative care in Acorn Woodpeckers (*Melanerpes formicivorus*) (Koenig and Mumme 1987) and Groove-billed Ani (*Crotophaga sulcirostris*) (Koford et al. 1990) increases the parents' longevity, but decreases the annual per adult production of fledglings. Posthatch aggregation of precocial young occurs in Common Eiders (*Somateria mollissima*), and in some predation regimens such aggregation contributes to increased duckling survival (Mendenhall 1975, 1979, Munro and Bedford 1977). Munro and Bedford (1977) speculate that mothers that combine broods also may benefit via longer reproductive lives. Cooperating California Quail parents provide an opportunity to examine whether the benefit of increased longevity can be realized without paying the cost of decreased per capita fledgling production.

When the young cannot initiate brood merging, the analysis of inclusive fitness benefits focuses on the generations that preceded the nestlings—the parents and older siblings. But precocial young initiate brood merging in some species. Deserted Barrow's Golden-eye ducklings (*Bucephala islandica*) join other broods, and benefit from the joined broods' maternal protection (Eadie and Lyon 1998). Canada Goose (*Branta canadensis*) goslings are sometimes reared in "gang broods" formed when the goslings of one set of parents join the goslings of another set (Sherwood 1967, Nastase 1983), and combined nuclear families including both sets of parents formed by goslings from two broods joining together have been observed (J. Eadie, pers. comm.; D. Lott, pers. observ.). The fitness consequences of those combined broods are not known, but if they increase the parent's lifetime reproductive success, the young are raising their own inclusive fit-

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